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CYTOTAXONOMIC STUDIES ON MOSSES OF THE CANADIAN ROCKY MOUNTAINS[1]

LEWIS E. ANDERSON AND HOWARD CRUM

Considerable information concerning chromosome numbers and chromosome behaviour is beginning to accumulate in the literature. Although far less than in higher plants, enough information is available on mosses to indicate that it will have a similar broad usefulness and wide application to problems of taxonomy and phylogeny. Too few mosses have yet been studied to permit any extensive application of chromosome data to solving problems of speciation or to understanding taxonomic limits, but a little progress has been made. The number and distribution of genera and families in which studies have been carried out are likewise too few and scattered for generalizations to be made, and much remains to be investigated concerning the basic cytology of mosses. Detailed studies of meiosis have been made in only two mosses, *Pleurozium schreberi* (Vaarama, 1954) and *Hedwigia ciliata* (Vaarama, 1954a). The present studies were initiated with the specific object of studying the chromosome number and behaviour in as large and representative a group of mosses from the Canadian Rocky Mountains as possible and of correlating the results with our present understanding of the taxonomy and geographic distribution of the species investigated.

Early chromosome studies of mosses dealt mainly with problems of cytogenetics and pure cytology (e.g., the Marchals, 1907–11; Allen, 1912; Wettstein, 1923–30; Barthelmess, 1938, 1941). The pioneering work of Heitz (1926, 1928) introduced badly needed improvements in techniques by adapting acetic carmine squash methods to moss materials, while Jachimsky (1935), a student of Heitz, perfected a method for making gametophytic squashes, which has enabled cytologists to study chromosomes in haploid somatic cells. Thus a way was opened for detailed studies on the morphology of somatic chromosomes and the making of comparative measurements.

There followed a number of chromosome studies of wild populations of mosses, including notable contributions by Shimatomai and Kimura (1936), Kurita (1937, 1939), Lowry (1948, *et seq.*), Vaarama (1949, *et seq.*), Tatuno (1951), Yano (1950, *et seq.*), Steere, Anderson, and Bryan (1954), Steere (1954), Bryan (1955, *et seq.*), Anderson and Bryan (1956), and Ho (1956). The earlier literature has been reviewed extensively by Lowry (1948), and several comprehensive reviews adequately summarize the more recent literature. They include papers by Sinoir (1952), Delay (1954), Steere, Anderson, and Bryan (1954), and Yano (1957a, 1957b, 1957c).

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The first attempt to correlate chromosome numbers with the taxonomy of mosses was probably the work of Heitz (1942), who pointed out in the genus *Mnium* the existence in nature of morphologically similar, haploid-diploid "paired" species (diploid-tetraploid in terms of the sporophyte). He also called attention to the fact that the haploid member of such paired species is heterothallic, while the diploid member is homothallic, and suggested that the diploid species arose aposporously from the haploid. The Marchals (1907–11) had, of course, earlier demonstrated this phenomenon on an experimental basis in *Amblystegium*. Lowry (1948) made the first truly cytotaxonomic study of a moss group in an extensive investigation of the somatic chromosomes of the genus *Mnium* in North America. He obtained cytological data which support the classical concepts of the morphological taxonomists. On the basis of chromosome number, for example, the segregation of the monotypic genus *Leucolepis* appears to be justified, and a possible relationship of the entire-leaved species of *Mnium* with the genus *Cinclidium* is also suggested. Lowry provided cytological evidence for segregating *Mnium pseudopunctatum*, which has 14 chromosomes and is monoicous, from *M. punctatum*, which has seven chromosomes and is dioicous, and also showed that *M. glabrescens* belongs in a 6- rather than a 7-chromosome series and could therefore be removed from the synonymy of *M. punctatum*. Tatuno (1951), however, found that *Trachycystis*, another generic segregate, could not be supported on the basis of chromosomal differences.

Bryan (1955) studied the chromosomes of ten North American species and varieties of the taxonomically difficult genus *Sphagnum*, including representatives from each of the subgenera, sections, and series recognized by Andrews (1937). She found that all species have a similar number of 19 large bivalents, except a single polyploid species in which the number, n=38, was found. In addition to the large bivalents, however, Bryan found remarkable differences among species in the number and behaviour of small bivalents, which she termed m-bivalents or m-chromosomes, after the terminology of Heitz (1928). With one or two exceptions she was able to correlate the number and behaviour of the m-chromosomes with Andrews' taxonomic groupings.

More recently, Bryan (1956, 1956a, 1957) has carried on extensive chromosome investigations of cleistocarpous and gymnostomous mosses, including *Bruchia, Pleuridium, Astomum, Acaulon, Phascum, Ephemerum, Nanomitrium, Physcomitrella, Aphanorhegma,* and *Physcomitrium,* and the peristomate genera related to them. Hers is the first attempt in mosses to use cytological information in evaluating the systematic position of genera and represents the most comprehensive application of cytological data to the taxonomy of mosses that has yet been made. Lowry (1954) has also made a significant contribution to taxonomy in his recent studies on chromosome numbers and relationships in the genus *Atrichum.* He demonstrated a strong correlation between bisexuality and polyploidy in this genus and was able to postulate the pattern of speciation in *Atrichum.* Anderson and Bryan (1956) have interpreted relationships between two species of *Fissidens* in the light of their chromosome complements, and in a later paper (unpublished) the same authors have studied polyploidy in the genus *Ditrichum* in relation to the geographic distribution of several North

American species. Yano (1957, 1957a, 1957b), in his latest series of studies on the cytology of Japanese mosses, discussed chromosome numbers and chromosome morphology of representatives of 22 families, including 63 genera and 139 species. In the most extensive cytological study of mosses to date, Yano made karyotypic comparisons of genera, families, and even orders. He found that five of the orders studied (namely, Fissidentales, Grimmiales, Dicranales, Eubryales, and Polytrichales) possess unique karyotypic characteristics. In all his investigations, Yano has emphasized sex chromosome morphology and the presence or absence of m-type and b-type chromosomes as comparative features.

The present investigation was undertaken as a part of an intensive program of field studies on the bryophytes of the Canadian Rocky Mountains sponsored by the National Museum of Canada during the summer of 1955. All the collections were made by the junior author, with the able and enthusiastic assistance of Mr. Wilfred B. Schofield, during the months of June, July, and August. The principal areas represented are Banff, Jasper, and Waterton Lakes National Parks, in Alberta, on the eastern side of the Continental Divide. Fewer collections were made on the British Columbia side in Kootenay and Yoho National Parks and also, outside the parks, in the vicinity of Mt. Robson. The choice of this area was particularly fortunate, not only because of the richness of the flora and the abundance of material, but also because the flora shares many species with two other areas in which moss cytology has been investigated, namely coastal north-central California (Steere, Anderson, and Bryan, 1954) and arctic Alaska (Steere, 1954). (A few collections were made on the trip from Ottawa to the mountains and have been included here.)

The extremely rugged topography and very high altitudes, together with an abundance of moisture, at least in protected valleys, favour a rich development of bryophytes in many ecological situations. The moss flora is essentially western montane, and, although large, it is not particularly distinctive. Most of the species, even the less common ones, are to be found elsewhere in boreal and arctic regions across Canada, Alaska, much of Siberia and northernmost Europe, and also southward at appropriate altitudes in the mountains of western United States. The number of species present is limited to a great extent by the scarcity of acid rocks; accordingly, the flora is markedly calciphilous in nature.

In the vicinity of Banff and Jasper the flora exhibits an abrupt transition at the Continental Divide with many Pacific Coast species growing on the western side of the Divide but not on the eastern. Farther south, however, in Waterton Lakes National Park, the two floras are intermingled on both sides of the Divide, perhaps because of the generally lower altitudes and less marked difference in moisture values on either side of the Divide, as well as the presence of a broad, relatively low route for plant migration through Crowsnest Pass.

Materials and Methods

Nearly all the cytological studies were made on spore mother cells (SMC) at meiosis. Living plants with developing sporophytes were collected by the junior author between June 9 and August 4, 1955, and shipped via airmail to the senior author at the botanical laboratories of Duke University in Durham, North Carolina, where all the cytological investigations were carried out. Immediately on collection, the plants were placed in air-tight plastic (polyethylene) bags. They were shipped as soon as field circumstances permitted, in some instances within a day or so, but frequently collections would accumulate for several days before being mailed. Little or no water was added to the plants before they were sent. It proved desirable to ship them in about the same condition as they were found in the field. When too wet they are susceptible to the action of bacteria and fungi.

The shipping distance was more than 2,000 miles. Although airmail was employed, all specimens had to pass through plant inspection stations, and delays were inevitable. A few shipments were received in Durham within 72 hours after collection, but normally material was in transit for four to as much as seven days and sometimes even longer. The condition of the living plants thus varied enormously upon arrival, depending not only upon the length of time they were in transit, but also upon the species involved, the moisture conditions at the time of collection, and most important, perhaps, the prevailing temperatures across the continent during the shipping period.

In spite of one of the hottest summers on record in North America, at least three-fourths of the collections arrived in good living condition, with healthy sporophytes. Upon receipt in Durham, the collections were unpacked, sorted, and placed in porcelain trays. They were then thoroughly moistened by spraying with an atomizer; care was taken, however, not to allow excess water to accumulate in the bottom of the tray. Each tray was then placed in a large plastic bag, left open at one end to permit the circulation of air, and stored in a refrigerator until the plants could be studied.

Inasmuch as the collections usually arrived in rather large batches, the problem of maintaining the plants in a healthy condition until they could be studied was a serious one. Also, the capsules of many collections proceeded through meiosis and became too old for study before they could be examined. A range of storage temperatures was tried experimentally, from 0°C. to 18°C. To our amazement the capsules from plants at 0°C. continued to develop, undergoing meiosis in a normal fashion and maturing spores, but at a much reduced rate. Eventually a temperature of 4°C. was used for storage, because of the availability of a walk-in refrigerator which could be illuminated continuously. As it turned out, however, it was not necessary to illuminate the plants, and some were maintained for several months with only sporadic and short exposure to weak light. They remained green, and the gametophytes of many collections continued growth. The only abnormal result noted was the appearance of numerous, small, axillary shoots which grew very rapidly and assumed the typically etiolated appearance of stems or branches developed in excessive shade. Meiosis was studied in a few species (e.g., *Orthotrichum, Fissidens, Tortula*) after storage at a low temperature for as long as four months.

This procedure proved to be very successful, for plants could be stored for long periods and examined periodically to determine the stage of capsule development. Slowing down the rate of meiosis and spreading out the process over a longer period of time worked to advantage because it made it easier to locate capsules with dividing sporocytes. Numerous populations were studied before and after storing, and no effects of the lowered temperatures on chromosome configuration or behaviour could be noted. With this procedure it was also possible to grow young capsules of many species to maturity. The capsules of some species failed to mature because they were attacked almost immediately by fungi, and within a short period of time a copious development of mycelium was noted. In other species, the capsules appeared to grow for a period and then succumbed to fungi. Capsules of other species, however, failed to grow even though they appeared to be free of fungal infection. The rate of capsule development varied enormously, depending on the species.

The fact that meiosis and spore maturation can occur at freezing temperatures is of considerable significance when it is considered that capsules of many species are normally produced during the rigorous winter months. Capsule production and maturation seem to occur in many mosses under conditions of environmental stress. Steere (1954), in his study of the chromosomes of arctic mosses at Point Barrow, Alaska, noted that capsule development began in several species in mid-June, when temperatures, measured at a point 2 cm above ground-level, averaged above 0°C. Meiosis was observed in some species as early as July 1, when temperatures at 2 cm ranged from 0° to 10°C., with a mean of about 5°C. The 2 cm level approximates the height to which the capsules would be elevated at the time of meiosis. The refrigerator temperature of 5°C. used in the present study is thus a close approximation of the mean temperature influencing meiosis at Point Barrow between June 15 and July 15.

Prolonged cold treatments (0°–3°C.) have been shown to influence the differential staining of chromosomes, at least in somatic cells. Heterochromatic segments become evident in chromosomes of cells dividing at low temperatures but are not visible at higher temperatures. Darlington and LaCour (1941) demonstrated this in embryo sac nuclei of *Fritillaria,* kept at 0°C., and several investigators, notably Wilson and Boothroyd (1944), have been able to distinguish heterochromatic segments in somatic chromosomes of *Trillium* kept at low temperatures but not in those kept at higher temperatures. Darlington and LaCour (1940) explained the phenomenon by assuming that at low temperatures the amount of nucleic acid synthesized is much reduced, with a resulting competition for it between euchromatin and heterochromatin. According to these authors, euchromatin is more successful, leaving the heterochromatin with a nucleic acid deficiency. Wilson and Boothroyd, on the other hand, postulated that the dark and light areas of euchromatin and heterochromatin, respectively, are due to differences in the degree of coiling; the euchromatin being more tightly coiled, more contracted, and therefore more heavily staining than the less contracted heterochromatic regions.

Levan (1942) has attributed the presence of constrictions in somatic chromosomes of *Secale* to low temperature. Of more significance, however, is the report by Panigrahi (1956) that at abrupt lowering of temperature chromosomes failed to pair in meiotic cells of *Cyclosorus repandulus*. In addition, Panigrahi noted the presence of tetraploid cells following abrupt low temperature treatment.

In the present study we did not employ the Feulgen's stain and thus made no comparisons of heterochromatic regions of chromosomes at high and low temperatures. In numerous mosses, however, we have compared meiosis in capsules maintained at 3° to 5°C. with that in capsules from the same population kept at temperatures between 20° and 26°C., and in no instance have we been able to detect differences in behaviour, morphology, or number of chromosomes. We feel perfectly confident, therefore, that the cold treatments employed in the present study did not modify chromosome numbers or influence meiotic behaviour to any appreciable extent. As previously noted, the only noticeable effect of low temperatures on meiosis is that spore mother cells remain in MI for a much longer period of time.

The cytological techniques employed in the present study were essentially the same as those which were described at length by Steere, Anderson, and Bryan (1954). Therefore, only a brief outline of the procedures will be given here.

Meiosis generally occurs in capsules that are still green, slightly translucent, and often with a faint line of colour at the junction of the operculum and the spore-bearing portion of the capsule. Promising capsules are selected, their contents squeezed out in a drop of Carnoy's solution (3:1) on a clean slide, and the SMC freed from the columella, if possible. If the SMC are difficult to separate from the columella, as much as possible of the latter is dissected away and the remaining tissue finely macerated. All extraneous material is removed, and the fixative is allowed to evaporate almost completely. A drop of acetic orcein (synthetic orcein saturated in 45 per cent acetic acid and filtered) is added before applying a cover slip. The slide is then heated almost to the boiling point several times in succession, and by gentle tapping the SMC are distributed evenly under the cover glass, in a single layer if possible. The slide is next inverted over bibulous or other absorbent paper on a sturdy, flat surface, and an even, firm pressure is applied to the back of the slide above the inverted cover glass. The amount of pressure applied depends on the fragility of the SMC and the amount of columella or other extraneous material remaining under the cover glass. Pressure is applied to accomplish three things: to spread out the chromosomes, to flatten the division figures so that the chromosomes lie in one plane, and to squeeze out oil bodies or other optically troublesome cytoplasmic inclusions. (Caution must be exercised, for if too much pressure is applied the bivalents may be separated, and with extreme pressure the cell wall may rupture.) The progress of this operation can be checked at intervals under the miscroscope.

When the preparation is completed, the cover glass is sealed with vaseline, and the SMC are studied immediately. In some instances the chromosomes may be slow to absorb the dye, and it may be necessary to store the slides overnight. It is possible to retain the preparation for several days or even weeks by storing the slides in a covered dish lined with moist filter paper, either at room temperature or in a refrigerator, depending on the degree of staining desired.

The investigations were made with a Spencer binocular, compound microscope with 1.4 mm., oil immersion, apochromatic objective, N.A. = 1.30, with an achromatic condenser, N.A. = 1.30, 15× compensating oculars, and a Kodak Wratten filter No. 74. The drawings were made with a camera lucida. Using a 30× ocular, a final magnification of ×4350 was obtained. The magnification of all published drawings has been reduced by one-half, and they are thus ×2175.

Samples of each colony from which counts were made were allowed to continue growth until some sporophytes were mature, for greater reliability in determination. A complete series of specimens has been deposited in the herbarium of the National Museum of Canada.

Observations

The results of the investigations will be described and discussed under the heading of each species. The species are grouped by families and arranged according to the system established by Brotherus (1924–25) in *Die natürliche Pflanzenfamilien.* An attempt is made to co-ordinate our results with those of other workers and to relate our observations to pertinent questions of phytogeography, ecology, floristics, and taxonomy.

In the interest of uniformity and in order that moss terminology may be co-ordinated with flowering plant usages, we use polyploid terms only as they apply to the sporophyte. Thus a "diploid species" to us is one in which the sporophytic cells contain the diploid or 2n number of chromosomes, just as in flowering plants. A "tetraploid species" thus is one in which the sporophytic cells contain the 4n number, a hexaploid, 6n, etc. Yano (1950, *et. seq.*) described polyploidy in mosses in terms of the gametophyte. Thus, in the Yano sense, a diploid moss is comparable to a tetraploid flowering plant, a triploid to a hexaploid, etc. This usage results in some confusion when comparisons are made, for example, between tetraploid flowering plants and tetraploid ("diploid") mosses.

The presence of small precociously disjoining bivalents as regular and constant components of the chromosome complements of many species of mosses is now well established. The terminology currently in use for these small bivalents is, however, much confused. Bryan (1955) reviewed this matter in considerable detail in connection with her studies of *Sphagnum*. She concluded that Heitz's term "m-bivalent" or "m-chromosome" is entirely applicable to the members of a complement, which are notably smaller, yet are segregated regularly in meiosis. This usage is followed in the present paper. There would seem to exist, however, another class of small bivalents which may or may not be comparable to m-bivalents. They are identical with m-bivalents in behaviour; i.e., they are distributed regularly at meiosis but are not outstandingly minute. We refer to these chromosomes as "small bivalents" and attribute to them no special structural or functional features. The significance of these chromosomes in mosses is entirely unknown, and very little is known of their nature.

Vaarama (1949, *et seq.*) used the term "accessory" chromosome to refer to these smaller chromosomes in mosses. This is an unfortunate designation, as the terms "accessory" or "supernumerary" chromosomes imply that they are extra chromosomes not homologous with those of the ordinary complement and are variable in number from individual to individual, although the number may be in equilibrium in a population (Östergren, 1947; Melander, 1950; White, 1951; Lewis, 1951). In contrast, the small chromosomes in mosses appear to be of constant occurrence with the species and, as Bryan (1955) pointed out, for this reason can be said to be regular members of the meiotic complement. They are apparently not comparable to the accessory or supernumerary chromosomes that have been described in numerous insects and a large number of flowering plants, including the B-chromosomes of corn, rye, and other plants (Hakansson, 1945; Müntzing, 1950). Until more is known concerning the nature and behaviour of these chromosomes in mosses, additional terms should not be coined to apply to the various types of bivalents.

FISSIDENTACEAE

Fissidens bryoides Hedw.

n=10 (Fig. 1–4)

This exceedingly variable and widespread species, studied from two separate collections from the same area, apparently has a tetraploid number, assuming that the number n=5, reported by Steere, Anderson, and Bryan (1954) for *F. limbatus,* is the basic number for the section Bryoideum. In contrast to those of *F. limbatus,* however, the chromosomes of *F. bryoides* show considerable variation in size, as is especially evident in figures 3 and 4, which show late metaphases that have been flattened by considerable pressure. In both figures the bivalents are about to separate, one large chromosome being held by a single terminal chiasma. Figures 1 and 2 show earlier metaphases, and the bivalent nature of several chromosomes can be discerned. The enormous size differences among the chromosomes of *F. bryoides* in contrast to the remarkable uniformity in size of those of *F. limbatus* are of interest in view of the fact that both species have been assigned to the same taxonomic section.

The American species of *Fissidens* section Bryoideum are so poorly understood that many specimens, particularly in the relationship of *F. bryoides, F. minutulus* Sull., and *F. viridulus* (Sw.) Wahl., cannot be positively identified. The range of *F. bryoides,* as given in Grout's revision of the Fissidentaceae of North America (1943), includes a wide area in Canada and the United States east of the Rocky Mountains, with disjunctions in Vancouver Island and Puerto Rico. It is obvious, however, from specimens named by Grout that his concept of *F. bryoides* was far from clear. According to the European and North American manuals, *F. viridulus* is dioicous, and its leaves are unbordered at the apex; *F. bryoides,* on the other hand, is autoicous and has the leaf border usually confluent with the costa at the tip. The Rocky Mountain plants are autoicous, sometimes with several antheridial buds on a single stem in the axils of lower leaves, and have leaves unbordered at the tip and, therefore, could be assigned to either species. We have seen many other Canadian collections with the same combination of characters and have come to the conclusion that the sexual condition is probably the only reliable difference between the two species. This was also the view expressed by Dixon (1924), who said, "The axillary male flowers form the character by which this species is most readily recognised from its allies; these are, however, sometimes very minute, and very rarely the male flower is found on a radical branch, according to Braithwaite." According to Nyholm (1954), *F. viridulus* in Fennoscandia is generally dioicous, but rarely autoicous plants are found. We suspect from her statement that anomalous plants similar to those from the Rocky Mountains occur also in Europe.

Although it is much too early to draw conclusions, the sections of the genus *Fissidens* thus far studied possess different chromosome numbers. They may be summarized as follows:

Section	Species	Chromosome Number (n)	Investigator
Bryoidium C.M.	*F. bryoides*	10	(reported herein)
	F. limbatus	5	Steere, *et al.* (1954)
Aloma C.M.	*F. pauperculus*	12	Steere, *et al.* (1954)
Serridium C.M.	*F. adiantoides*	(19) 20	Heitz, 1928
		24	Anderson & Bryan (1956)
	F. cristatus	16	Yano (1951a)
		16	Sannomiya (1955)
		12	Anderson & Bryan (1956)
	F. japonicus	16	Yano (1951a, 1957a)
	F. taxifolius	9	Sinoir (1952)
		12 ($2n=24$)	Moutschen (1952)
Pachyfissidens C.M.	*F. planicaulis*	14	Yano (1957a)

The differences in chromosome number of Section Serridium are striking, and perhaps similar inconsistencies will appear in other sections when more species have been studied. It is especially significant that *F. cristatus,* a species widely distributed in eastern North America and throughout most of Europe and a large part of Asia, has different chromosome numbers in Asia and the United States. Also, *F. japonicus* Dozy & Molk., a close relative of *F. cristatus,* has the same chromosome number as the Japanese populations of the latter. The presence of intraspecific chromosome races on different continents is a problem that will have to be seriously reckoned with in evaluating specific differences among continental segregates or vicarious representatives.

DITRICHACEAE

Ceratodon purpureus (Hedw.) Brid.

$n=13$ (Fig. 5–6)

The chromosome number of this ubiquitous and weedy moss has been reported numerous times, and with the exception of Heitz' original report of 11 to 12 bivalents, all investigators have observed the same number, n=13. Previous workers, without exception, mentioned a large bivalent, nearly always described as a heterochromosome and assumed to be involved in sex determination (Heitz, 1928; Jachimsky, 1935; Shimatomai & Kimura, 1936; Steere, *et al.*, 1954; and Steere, 1954). A similar large bivalent was observed in the Rocky Mountain population, but in spite of careful observations, no evidence could be found to support the notion that it is a heterochromosome. Occasional figures were observed (Fig. 6) in which one of the dyads appeared to be somewhat larger than its homologue, but such an appearance is probably due to the unsymmetrical orientation of the bivalent. Anaphase I and anaphase II figures revealed no appreciable differences in the size and appearance of this large chromosome. In order to settle the problem of a possible heterochromosome, somatic chromosomes from antheridial plants should be compared carefully with those from archegonial plants.

Distichium capillaceum (Hedw.) BSG

n=14, n=28 (Fig. 7–13)

Apparently two distinct chromosome races occur in this species. A population from Carthew Lakes in Waterton Lakes National Park was found to be diploid, but two tetraploid populations were discovered: one grew along the Bow River near Banff, the other in Jasper National Park at Sunwapta River. In the only previous study of this species, Steere (1954) reported the number n=14 in Alaskan plants collected near Point Barrow. Thus, of four populations so far studied, two are diploid and two tetraploid. The chromosomes of both diploid and tetraploid are remarkably alike in size and show little or no variation in morphology. (The SMC of the tetraploid populations, however, are nearly twice as large as those of the diploid population, although no differences in spore size could be detected. This point is discussed below.) Meiosis in the tetraploid populations is completely regular, and no multivalent associations, lagging chromosomes, or anaphase bridges were observed that might be indicative of recent polyploidy. The tetraploid condition would therefore seem to be well established and completely stable.

In the tetraploid population from Bow River, one of the bivalents exhibited an unusual structure in that the chromonemata apparently are not so condensed as in the other bivalents, and little (or, at least, much less) matrix surrounds each of the two homologous chromonemata (Fig. 9, 11; in fig. 10 the same bivalent is apparent as a star-shaped body). In anaphase the half-bivalents separate and move to the poles as do the other chromosomes. A comparable bivalent was not observed in the other tetraploid or in the diploid populations. The significance of this unique bivalent is not known.

Distichium capillaceum is extremely common in northern latitudes around the world and is to be found commonly at higher altitudes in the mountains southward in both northern and southern hemispheres. It occupies natural habitats and does not seem to be a weedy species, in spite of its very wide distribution and local abundance. It varies throughout its range in stature and in leaf length, and its gross aspect varies accordingly, but these variations seem to be environmentally induced with no apparent geographic isolation of extremes. The size and shape of the capsules are also variable throughout the range, with no geographic correlation which would suggest a degree of genetic segregation. There appear to be no structural characters suggesting a need for a redefinition of specific limits or a possibility of dividing the species into geographic subtaxa.

Quantitative comparisons are difficult in a species which has a broad ecological tolerance and is obviously much altered by environmental differences. The plants in all three collections used in this study were autoicous, the antheridia being produced laterally in one or more buds at some distance below the perichaetium. It should be noted, however, that more than 20 fruiting plants in the diploid population were dissected before a single autoicous plant was found; five plants with 2 to 3 lateral antheridial buds were found, but the tips of the plants seemed to be immature, and it was presumed that perichaetia would eventually have formed in the expected terminal position on such plants. (Unfortunately, it was not possible to determine the sexual condition of the individual plants from which the chromosome counts were made. It is remotely possible, therefore, that the few clearly autoicous plants found in the diploid population could be tetraploids. The chromosome count for the diploid population was established on the basis of studies from four plants.)

No differences in the size of leaf cells could be demonstrated. The diploid plants are very small and compact with leaves only 1.5 to 2 mm long, setae 7 to 9 mm, capsules 1 to 1.5 mm and more or less ovoid, and spores 19 to 22 μ in diameter. In Europe this form has been called *D. capillaceum* var. *compactum* (Hüb.) Podp. Our observations of considerable material, both in the laboratory and in the field, lead us to agree with Nyholm (1954), who said, "In arctic-alpine regions there are forms with shorter leaves in more compact tufts; the capsule also is often shorter. The extreme form is described as var. *compactum*. . ., but there is every gradation between it and the type." The diploid population came from a bleak, windswept, alpine situation at about 7,500 feet altitude, considerably higher than the tetraploid populations.

The gametophytes of the tetraploid plants collected at Sunwapta River are rather small and compact with leaves only 1.5 to 2 mm long, thus resembling somewhat the diploid plants, but the setae are 12 to 14 mm long, and the capsules are cylindrical and about 2 mm long; unfortunately, no mature spores were seen. In the other tetraploid specimen, from Bow River, the leaves are 2.5 to 3.5 mm long, the setae 15 to 18 mm, the cylindrical capsules 2 mm, and the spores 27 to 28 μ in diameter. It should also be noted in this connection that the SMC in both tetraploid populations are at least twice as large as those of the diploid. The difference in spore size may be highly significant, but how this may be associated with polyploidy and what taxonomic significance it may have will have to await study of other polyploid populations of *Distichium*. It is possible, even though meiosis is regular, that these plants are polyploids of very recent origin, and after a few generations, with cytological stability, the differences in spore size will disappear. Vaarama (1955) has recently postulated such stabilization and loss of *gigas* characters in *Funaria*.

Distichium seems clearly a member of the Ditrichaceae on the basis of sporophytic characteristics, but the strikingly distichous arrangement of the leaves and the extreme roughness of the leaf awns indicate only a distant relationship with the other subfamilies of Ditrichaceae. This distant relationship is nicely reflected in the chromosome situation, in so far as it is known: the Ceratodontoideae (*Ceratodon* and *Saelania*) and some of the Ditrichoideae (*Pleuridium* and *Ditrichum*) have 13 (or 26) bivalents (*Trichodon*, of the Ditrichoideae apparently has 12), whereas the Distichioideae have 14 (or 28 or 42). The family may be summarized as follows:

Ditrichoideae		
Pleuridium acuminatum Lindb.	n=26	Bryan (1956a)
P. bolanderi C. M.	n=26	Steere, *et al.* (1954)
P. ravenelii Aust.	n=13	Bryan (1956a)
P. subulatum (Hedw.) Lindb.	n=13	Bryan (1956a)
Trichodon cylindricus (Hedw.) Schimp.	n=12	Steere (1954)
Ditrichum curritucki Grout	n=13	Bryan (1956a)
D. henryi Crum & Anderson	n=13	Crum & Anderson (1956)
D. pallidum (Hedw.) Hampe	n=26	Bryan (1956a)
D. schimperi (Lesq.) Par.	n=26	Steere, *et al.* (1954)
Ceratodontoideae		
Saelania glaucescens (Hedw.) Broth.	n=13	Steere (1954)
Ceratodon purpureus (Hedw.) Brid.	n=13	Numerous investigators
Distichioideae		
Distichium capillaceum (Hedw.) Brid.	n=14	Steere (1954)
	n=14, 28	(reported herein)
	n=42	Steere (1954)

DICRANACEAE

Dicranella crispa (Hedw.) Schimp.

n=14 (Fig. 14, 15)

The haploid chromosome number of this species was reported by Steere (1954) to be 15, and although we found many sporophytes with this number, we were able to identify the chromosomes as 13 bivalents plus two half-bivalents that had separated precociously. An appreciable number of figures were observed in which 14 bivalents were clearly distinguishable, so that we feel confident in reporting for the Rocky Mountain population the number, n=14. The chromosomes of *D. crispa* are nearly uniform in size except for one large bivalent with a characteristic and recognizable configuration in prometaphase and metaphase stages. Apparently the centromere is subterminal, and in figure 15 it can be seen in an early metaphase configuration with apparently two chiasmata.

Brotherus (1924–25) included this species in *Anisothecium* and assigned *D. subulata,* to which it is very closely related, to *Dicranella,* thus placing them in two separate subfamilies! Both species have a well-developed annulus, and largely for that reason *D. crispa* seems misplaced in *Anisothecium.* Also its more or less sheathing leaves, often subsquarrose at the tips of the stems or somewhat below them, are hardly striking enough or significant enough to warrant separation from *Dicranella. Anisothecium* is one of the weakest of all segregate genera, in so far as North American species go; certainly the absence of an annulus and a relatively large peristome do not warrant shifting *Dicranella varia* (Hedw.) Schimp., for example, into another genus, not to mention another subfamily. A stronger argument could perhaps be presented for the segregation of *Anisothecium schreberianum* (Hedw.) Dixon because of its strongly sheathing leaves with very squarrose tips, but it has little in common with many other species, such as *Anisothecium persquarrosum* (Dus.) Broth. (Crum, 1952), which Brotherus also included in *Anisothecium*.

Only three supposed members of *Anisothecium* have been studied cytologically: Steere, Anderson, and Bryan (1954) reported 14 chromosomes for *Dicranella varia*, and Steere (1954) found 15 in *D. grevilleana* and *D. crispa*, but the latter can, by interpretation of his published figures, be reconciled to our count of 14 for both *D. crispa* and *D. subulata*, and very likely all his counts could be interpreted in the same way. If so, the cytological evidence thus far uncovered would give no basis for maintaining *Anisothecium* as a genus in North America.

There is a comparable lack of agreement in chromosome number in *Dicranella* proper. Steere (1954) reported for *D. cerviculata* n=15, while Yano (1957a) found the number n=13 for *D. heteromalla*, a closely related species, and we have found 14+1 in *D. subulata* (*see* below). Yano (l.c.), who studied somatic cells, reported a pair of heterochromosomes in the complement of *D. heteromalla*, based, however, on size differences of their respective heteropycnotic bodies. Furthermore, he postulated that the species is a hypodiploid, evolved, according to Yano, by the loss of one or two small chromosomes; the evidence for this is obscure. These are the only species in *Dicranella*, exclusive of *Anisothecium*, for which chromosome counts have been published. The lack of agreement among investigators points to the fact that there is probably a high degree of aneuploidy within the genus (in the broad sense). Additional chromosome studies should therefore add appreciably to our understanding of this difficult group.

Dicranella subulata (Hedw.) Schimp.

n=14 + 1 (Fig. 16–21)

No previous cytological studies are known for this species, which is very closely related to *D. crispa*, differing essentially in having curved, inclined capsules and leaves usually somewhat secund. The meiotic chromosomes are exceedingly difficult to interpret because of the presence in prometaphase and metaphase of a variable number of small, faintly-staining chromosomes. There are clearly 14 large, dark-staining bivalents, but the number of smaller chromosomes ranges from one to four. Most MI figures show three of the smaller chromosomes (Fig. 18, 20, arrows pointing to the three faintly-stained chromosomes). It was eventually observed, however, that the variable number of the smaller bodies resulted from the precocious disjunction of a single bivalent into two half-bivalents, one of which divides into its respective sister chromatids. Thus the three lightly-staining chromosomes observed in many sporocytes represent one half-bivalent and two sister chromatids derived from a single small bivalent.

Occasionally the half-bivalent also divides precociously so that a tetrad of small light-staining chromosomes consisting of two pairs of sister chromatids is produced (Fig. 17). Figure 16 is a drawing of a prometaphase figure in which 14 larger, dark-staining bivalents are visible, and the small, light-staining bivalent has not disjoined. In staining reaction and behaviour the small bivalent is identical with the m-chromosomes or m-bivalents in *Sphagnum* (Bryan, 1955), except that the m-bivalent of *D. subulata* is appreciably larger than those of *Sphagnum*. The dissociation of the m-bivalent in *D. subulata* is illustrated in figures 16 to 21. In figure 16, the m-bivalent is beginning to separate into its respective half-bivalents, whereas in figures 18 and 20, which are side and polar views respectively of MI, one of the half-bivalents has separated into its respective sister chromatids, while the other is still undivided. This results, as previously noted, in 14 larger, darkly-stained bivalents plus three small, faintly-stained chromosomes. Finally, in figure 19, the second half-bivalent is shown dividing into its respective sister chromatids. Figure 21 shows a flattened anaphase I, in which 14 half-bivalents and the two sister chromatids derived from the m-half-bivalent can be counted at each pole. The sister chromatids at each pole are indicated by arrows.

This behaviour is in striking contrast to that observed in *D. crispa*, a close relative, in which there was no evidence of an m-chromosome. It is significant, however, that in both species there is a conspicuously large bivalent that can be identified from cell to cell.

Amphidium lapponicum Schimp.

n=16 (Fig. 22)

This count confirms Vaarama's report (1950) based on a Finnish population. The systematic position of the genus *Amphidium* is in some doubt. Brotherus (1924–25) included *Amphidium* in the subfamily Rhabdoweisioideae of the Dicranaceae, and other European authors (Jensen, 1939, for example) have followed his lead. Grout (1946) included the genus in the Orthotrichaceae and said that "its alliances are much more clearly with *Ulota* and *Orthotrichum*. The smooth, cucullate calyptra is the only character at variance with this position. This also occurs in *Drummondia*, but the peristome in that genus helps to indicate its affinities." (Grout seems to have overlooked the fact, also useful in his argument, that most species of *Zygodon* also have smooth, cucullate calyptrae.) Dixon (1924) and others welded the genus more firmly to the Orthotrichaceae by including it in the genus *Zygodon*. Although Dixon's generic concepts were extremely broad, his comments are pertinent to a consideration of relationships: "Although the sub-immersed capsules of *Z. lapponicus*, of a thicker consistency and with a wider mouth, give the plant a very different habit from that of the species with longer setae, it is only a question of a very slight shortening or lengthening of the seta; *Z. Mougeotii*, indeed, in this respect approaches the species usually included under *Zygodon*, and the differences resolve themselves into slight distinctions in the form of the capsule, hardly sufficient to carry generic rank when in so many particulars the plants are closely allied."

The leaves of *Zygodon* and *Amphidium* are indeed very similar, but there are other, perhaps more fundamental reasons for relating *Amphidium* to the Orthotrichaceae. The small, lateral, antheridial buds of *Amphidium lapponicum* are very similar to those of many autoicous species of *Orthotrichum*. The small, immersed capsules, strongly constricted below the mouth when dry, are also manifestly characteristic of the Orthotrichaceae, both in appearance and in structure. The stomata at the base of the urn are similar to those of many species of *Orthotrichum*, for example, as are the differentiated bands of cells making up the ribs of the capsule. The differentiated perichaetial leaves of *Amphidium lapponicum* suggest those of *Hypnodon* and *Rhachitheciopsis* of the Orthotrichaceae and are anomalous in the Dicranaceae. The absence of a peristome is unusual in both families, but several species of *Zygodon* also lack a peristome, and in any case, its absence in *Amphidium* can probably be interpreted as a result of evolutionary reduction, as in many other phyletic lines in which most, but not all species or genera may be peristomate.

We feel that *Amphidium* has little or nothing to do with the Dicranaceae. The situation is complicated, however, by the considerable resemblance of *Amphidium* and *Rhabdoweisia denticulata* (Brid.) BSG, which has very similar stomata at the base of the urn and cells differentiated in bands corresponding to the ribs of the capsule wall in exactly the manner so characteristic of the Orthotrichaceae, and the small gametophytes are in many ways similar to various members of the Orthotrichaceae. The peristome teeth are not forked or pitted-striate, as in the great majority of Dicranaceae. All in all, there seems to be no reason, other than tradition, for *Rhabdoweisia* to be included in the Dicranaceae.

The relationships of *Rhabdoweisia* with the Orthotrichaceae were noted by Loeske (1910, p. 95), who said, "Die morphologischen Strahlungen von Rhabdoweisia-Charakter erstrecken sich sehr weit. Das charakteristiche Blatt und das Zellnetz kehren, tratz verschiedener Modifikationen sofort kenntlich, wieder bei Amphidium, Zygodon, Ulota, Orthotrichum, Amphidium, besonders A. lapponicum, zeigt auch habituell sehr grosse Verwandtschaft. Die bei allen mehr oder weniger gefurchte, selten glatte Kapsel hebt die Verwandtschaft weiter hervor. Alle Untersuchungen befestigten mein Überzeugung, dass die Familie der Orthotrichaceae im System den Rhabdoweisiaceae benachbart sein müssen, deren 'höhere' Stufen sie bilden."

Malta (1926, p. 28), in his world monograph of the genus *Zygodon*, was of the opinion that *Amphidium* is more closely related to *Rhabdoweisia* than to *Zygodon*, but also pointed out that, with the exclusion of *Amphidium* from the Orthotrichaceae, *Zygodon* is the only remaining genus of that family with close affinities to the Dicranaceae and the Pottiaceae.

It seems to us, on morphological grounds, that *Amphidium* would most logically be included in the Orthotrichaceae, except for its resemblance to *Rhabdoweisia*. Pending further cytological information, we feel that it is more realistic to recognize the family Rhabdoweisiaceae, including *Rhabdoweisia*, *Rhabdoweisiella*, and *Amphidium*, in close relationship to the Orthotrichaceae. The cytology of *Zygodon* would be most interesting in this connection.

Many of the genera of Dicranaceae show a similarity of chromosome behaviour. Bryan (1956a) has shown that in *Bruchia*, *Trematodon*, and *Dicranum* the configurations are difficult to evaluate, the chromosomes have a strong tendency to clump, and if an attempt is made to spread them out by tapping or pressing on the cover glass, the chromosomes become conspicuously stretched and attenuated. In extreme cases the chromosomes may break, or the distal portions become attenuated into a small chromatin fragment connected only by a thread. Bryan observed this behaviour to a greater extent in *Bruchia* but found a similar tendency in other genera. We have found similar behaviour in *Cynodontium*, *Dicranoweisia*, *Oncophorus*, and *Dicranum*. It is significant, therefore, that the chromosome configurations in *Amphidium* do not resemble those observed in other members of the Dicranaceae, a fact which also supports the morphological reasons for excluding *Amphidium* from the Dicranaceae.

The chromosome number is not especially helpful in this instance because of the lack of correlation between the numbers that have been reported in the Dicranaceae and the current generic groupings. The Trematodontoideae, with *Bruchia* and *Trematodon*, have the numbers n=14, 14+1, and 28; the Anisothecioideae, with three species of *Anisothecium* reported, have the number n=15 (probably 14+1); the Campylopodioideae, with only two species in the genus *Dicranella* known, have the numbers n=13 and 14+1; a single species (*Paraleucobryum*) indicates that the Paraleucobryoideae have n=12; the Rhabdoweisioideae have the numbers n=12 and 16, while the large subfamily Dicranoideae have the numbers n=10, 11, 12, 14, 15, and 23, the latter an obvious polyploid. The number n=16 found in *Amphidium*, therefore, is not an improbable number for the Dicranaceae in view of the rather wide aneuploid series known for the family. On the other hand, it has the highest basic number yet reported for the Dicranaceae. In the Orthotrichaceae, however, a considerable degree of aneuploidy can also be demonstrated. Numbers of 6, 11, 13, and 18 have been found in *Orthotrichum* and 8, 19+2, and 21+1 in *Ulota*.

Cynodontium strumiferum (Hedw.) DeNot.

n=14 (Fig. 23–25)

Vaarama (1950a) has reported the number, n=15, for plants from Finland, but the Rocky Mountain material does not agree with his observations. We were able to investigate two populations, both collected at the Continental Divide on the Windermere Highway (just inside Banff National Park). Figure 23 shows convincingly 14 bivalents, each of which exhibits centromere activity. There are 13 large bivalents, and one smaller bivalent that tends to divide prematurely (Fig. 24, 25); in figure 24, 13 large bivalents are shown with spindle attachments and the smaller bivalent in the process of disjoining. Steere (1954) reported the number n=14 for *C. alpestre* but stressed the individuality of a few bivalents which he was able to recognize from sporocyte to sporocyte. The meiotic chromosomes of *C. strumiferum*, however, are quite uniform in size except for the one small bivalent.

While the generic relationships are not particularly close, the form and behaviour of the chromosomes of *C. strumiferum* strongly resemble those of *Dicranella*. Compare, for example, figure 23 with figure 16, and figure 25 with figure 17. The chromosomes of both complements are strongly condensed, have mostly terminal centromeres, are easily spread apart, and show little or no tendency to be sticky. They differ rather strikingly from the chromosomes of related genera which, as has already been pointed out, are sticky, tend to clump rather badly, and are difficult to spread apart; also, in *Oncophorus,* for example, more of the chromosomes have median or submedian centromeres (Fig. 28) and thus resemble the chromosomes of *Dicranum* (Fig. 29–37). This is interesting in view of the fact that Williams (1913) and Grout (1928–40), and consequently most American bryologists, group together in *Oncophorus* both *Cynodontium* and *Cnestrum,* which are generally segregated by European authors, as well as *O. virens* (Hedw.) Brid., *O. wahlenbergii* Brid., and *O. rauei* (Aust.) Grout, which belong to *Oncophorus* in a strict sense and, in our opinion, are not generically allied to *Cynodontium* or *Cnestrum* at all. It is hoped that cytological information on *Cnestrum* will throw further light on what appears to be a very weak segregate from *Cynodontium.*

Dicranoweisia crispula (Hedw.) Schimp.

n=11 (Fig. 26–27)

This species, very common in the Canadian Rocky Mountains, was studied by Steere, Anderson, and Bryan (1954), who reported the number, n=11, for a Californian population. They found the chromosomes well defined and easily identifiable. The Rocky Mountain material, however, studied from two populations (from Sunwapta Falls and Lake Louise), was very difficult to interpret. Several capsules with dividing sporocytes were investigated from each population. The chromosomes were usually clumped tightly and were sticky and difficult to spread apart. Figures 26 and 27, drawn from the best figures observed, show nine bivalents rather clearly, but the other two bivalents are associated in pairs connected by thin chromatic strands. In figure 26 the tendency for two of the bivalents to remain associated late into metaphase is also indicated. The striking contrast in behaviour between these populations and the Californian one may be a result of environmental differences. (There is also the possibility that extreme heat conditions during transit across the continent may have affected the plants. As these plants were stored for a longer time than most of the material investigated, this also may have affected the chromosome behaviour.)

Oncophorus virens (Hedw.) Brid.

n=14 (Fig. 28)

This account agrees with Steere's report (1954) of n=14 for both *O. virens* and *O. wahlenbergii* Brid. in Alaska, although Steere's anaphase figure shows 12 chromosomes in one group and 14 in the other group. The fact that at least one and sometimes two bivalents separate prematurely could lead to mistaken interpretation. The prematurely dissociating bivalents, however, are about the same size as the others, none of which exhibits much variation in size. As previously noted, the meiotic chromosomes of *Oncophorus* and other mosses of the Dicranaceae are sticky and difficult to spread apart. Considerable pressure on the cover glass was necessary and doubtless contributed to some of the bizarre shapes assumed by prometaphase and metaphase chromosomes. We were never able to secure good preparations, and Steere must have experienced similar difficulties, for (as noted above) his illustration (1954, p. 99) reveals 12 and 14 chromosomes at the two poles of an anaphase I figure.

In North America *Oncophorus* (in a restricted sense) is a homogeneous group of three species, *O. virens, O. Wahlenbergii,* and *O. rauei* (Aust.) Grout. Cytological information on the last-named species would be welcome because of its checkered history. It was originally described from sterile material. Williams (1911) erected for it a monotypic genus *Austinella* and compared it with *Trichostomum,* in the Pottiaceae. Later (1913) he transferred it to the Dicranaceae, next to *Symblepharis,* and Brotherus (1924–25) included it in *Symblepharis.* More recently the sporophyte has been discovered, and Grout (1928–40), on transferring the species to *Oncophorus,* reported that the sporophyte is similar to those of *Oncophorus wahlenbergii* and *O. virens.*

Somatic chromosomes of both *O. wahlenbergii* and *O. virens* have been studied by Yano (1957a). In the former he described two large H-chromosomes, which exhibit different "aspects" in heteropycnosis. On this basis he concluded that *O. wahlenbergii* is a "diploid" (tetraploid in the sporophytic sense) that has been derived from a "monoploid" (i.e. diploid) species. He claims to have been able to pair up the other members of the chromosome complement. So far as known, all of the species of both *Oncophorus* and *Cynodontium* are autoicous. Postulation of a dioicous ancestor with a single H-chromosome, therefore, is difficult.

Dicranum fuscescens Turn.

n=12, n=24. (Fig. 29–34)

This exceedingly variable and widespread species has not previously been studied cytologically. We were gratified to be able to investigate 10 populations. Although most populations were observed to have the number n=12, the most common number found in *Dicranum,* at least in North America and Europe, a single population proved unquestionably to be tetraploid, with the number, n=24 (Fig. 31, 32). This population was found at Baker Creek about 10 miles east of Lake Louise.

All the collections studied here seem to fall easily within the specific limits of *D. fuscescens,* and although some of the colonies are rather slender and weakly developed so that the aspect is quite different, no quantitative differences of any importance were observed. The tetraploid plants differ in no way from several other populations either in appearance or in measurements of cell diameters, spores, lengths of leaves, setae, capsules, or opercula. Oddly enough, although the spores are no different from those of several of the other populations, the SMC of the tetraploid are smaller than those of the diploids. The significance of this is not known, but it is the opposite to the size relation noted in the two chromosome races of *Distichium capillaceum* reported above.

Several genera of mosses have been shown to possess paired diploid-tetraploid species, but only a few species are known to have both diploid and tetraploid populations in nature. This is surprising in view of the ease with which polyploids can be produced in the laboratory through apospory (see, for example, Marchals, 1911–12; Wettstein, 1923, *et seq.;* Heitz, 1945). Heitz (1942) reported a natural triploid population of *Atrichum undulatum;* Steere, Anderson, and Bryan (1954) found both tetraploid and hexaploid populations of *Tortula princeps;* and Vaarama (1950a, 1955) discovered a tetraploid race of *Funaria hygrometrica.* Yano reported diploid and tetraploid races in *Philonotis socia* (1957a), *Brachythecium brotheri* (1957b), *Thamnium sandei* (1957c), and *Polytrichum attenuatum* (1957c). Vaarama (1949) found polyploid areas in the archesporia of *Rhacomitrium ramulosum* and *Grimmia muhlenbeckii;* in both cases, however, most of the sporocytes were normally diploid.

It has been assumed that polyploid gametophytes may be produced occasionally in nature by the accidental regeneration of sporophytes. Since the sporophyte is genetically bisexual, it follows that a gametophyte produced from it without reduction division would also be bisexual. The tetraploid plants reported here, however, are clearly dioicous, with both male and female plants of equal size and similar appearance mingled together in the same tuft. This indicates that naturally produced tetraploid mosses are not necessarily monoicous and that they may arise by some means other than apospory. At the same time, apospory may well play a part in nature, as indicated by a number of species pairs; in *Mnium,* for example, in which the gametophytes of diploid plants are dioicous and those of tetraploids monoicous (Heitz, 1942; Lowry, 1948).

Of cytological interest is the fact that in all the diploid populations of *D. fuscescens* the meiotic chromosomes at MI appeared relatively large and somewhat sticky and were not always easy to spread apart. In the tetraploid, on the other hand, the chromosomes were smaller, more discrete and condensed, and showed little or no tendency to stick together at the metaphases. They were, as a consequence, easy to spread and, in spite of the higher number, much easier to count.

There was little or no evidence of secondary association or secondary pairing of chromosomes in the tetraploid population. In mosses this is often difficult to interpret, as the chromosomes are nearly always tightly clumped at metaphase and require pressure on the cover glass or slide to spread them apart. Also, not infrequently, evidence of secondary pairing was observed in diploid populations. In fact, some tendency toward secondary association is nearly always present during meiosis in most mosses. Yano (1957c) noted many secondary pairings in tetraploid sporocytes of *Thamnium sandei,* although he found that meiotic divisions took place regularly, and perfect spores were produced. He failed to note whether secondary association was observed in diploid populations.

In a single capsule from one population, the majority of figures contained what appeared to be a chromosome fragment (Fig. 34). At first it was believed to be a small m-bivalent, but later observations indicated that it did not disjoin nor did it exhibit regular anaphasic movement. Apparently, the fragment remains in the equatorial plate zone (Fig. 33) and fails to be included in either daughter nucleus. No second division figures were present in the single capsule in which the fragment was observed, and so it was not followed through meiosis. Likewise it was not observed in any of the other capsules of this species.

Dicranum groenlandicum Brid.

n=12 (Fig. 35, 36)

A number of preparations were made of this species, and, in contrast to *D. fuscescens*, satisfactory figures were few. Meiotic chromosomes are prone to clump into three groups of apparently four bivalents each, and extreme pressures in the preparation of slides are required to separate the chromosomes into discrete bivalents. (Material of this species, however, was received in rather poor condition, and so it is not improbable that the clumping of the chromosomes can be attributed to unhealthy capsules. Some had obviously been attacked by bacteria, and others had suffered injury.) One sporocyte, however, was observed in diakinesis (Fig. 36), a stage rarely observed in mosses, and a definitive count was thus possible. As can be seen from this figure, 12 bivalents are present. A metaphase figure in which the bivalents were aggregated into two groups is shown in figure 35, after they were separated by force and spread out over the SMC.

No small bivalents or m-chromosomes were observed, and the large conspicuous bivalent observed in *Dicranum* by some investigators, and described as a heterochromosome, was not seen. (Such a heterochromosome is shown in fig. 29, 30, in sporocytes of *D. fuscescens.*)

No previous counts have been made of this species, but Steere (1954) reported n=13 for *Dicranum elongatum*, which is very closely related to *D. groenlandicum* and intergrades with it in a most perplexing manner. The extremes are rather well differentiated, however, and undoubtedly the present material belongs here rather than at the *D. elongatum* end of the scale.

Thirteen is an unusual number in *Dicranum*, and it seems possible that Steere's count for *D. elongatum* should be interpreted as 12+1, instead. This is suggested by Steere's statement that the "chromosomes grade rather imperceptibly from large to small, and the smallest pair tends to disjoin prematurely." Vaarama (1950, 1950a) reported small m-type chromosomes in *Dicranum majus*, and we have observed them in *D. strictum* (see below). In view of the close taxonomic position of *D. groenlandicum* and *D. elongatum*, it would be most interesting to know if the latter differs consistently in the possession of a single small, precociously separating chromosome lacking in *D. groenlandicum.*

We are grateful to Dr. Elsa Nyholm who has kindly confirmed the determination of the material as *Dicranum groenlandicum.*

Dicranum strictum Schleich.

n=12+2 (Fig. 37)

Unquestionably the chromosome complement of this species consists of 12 large bivalents and thus agrees with the number reported for the genus by most investigators. The number of small chromosomal elements observed ranged from three to eight, but not enough division figures were found to follow the behaviour of the small chromosomes accurately. It is believed, however, that in addition to the 12 large bivalents two small bivalents dissociate prematurely into four half-bivalents (Fig. 37). These half-bivalents apparently divide into their respective sister chromatids before the large bivalents disjoin at MI. The number of small chromosomal elements observed depends, therefore, upon how far disjunction has proceeded. Those sporocytes in which three small chromosomes were observed are interpreted as having one small bivalent undissociated and two half-bivalents, those with four small chromosomes (Fig. 37) as having four half-bivalents, and those with higher numbers as having varying numbers of sister chromatids. A somewhat different interpretation has been offered by Vaarama (1950, 1950a) and later confirmed by Steere (1954), for *D. majus.* They reported the presence of 13 large bivalents, one of which "breaks up" into two to five "segments." *Dicranum majus* and *D. strictum* are not closely related, however, and the behaviour in the two species may not be the same.

Some authors assign *D. strictum* to the genus *Orthodicranum,* which has been segregated essentially on the basis of more or less erect capsules. The chromosomes of this species provide no support for an otherwise poorly justified segregation.

Bryan (1956a) has discussed chromosome numbers in relation to the subfamilies of the Dicranaceae, and Yano (1957a) has recently made comparisons of somatic chromosomes among several genera in this family, notably *Dicranum* and *Oncophorus.* A summary of the chromosome numbers of genera grouped according to subfamily is quite revealing:

Subfamily Trematodontoideae
    Bruchia, n=14, 15, 28
    Trematodon, n=28

Subfamily Anisothecioideae
    Anisothecium, n=14, 15

Subfamily Campylopodioideae
    Dicranella, n=13, 15

Subfamily Paraleucobryoideae
    Paraleucobryum, n=12

Subfamily Rhabdoweisioideae
    Amphidium, n=16
    Rhabdoweisia, n=*ca.* 12

Subfamily Dicranoideae
    Cynodontium, n=14, 15
    Dicranoweisia, n=11
    Oncophorus, n=14
    Dicranum, n=11, 12, 12+2, 12+5, 14

There is, thus, not a particularly strong similarity in chromosome number among genera of the same subfamily. The numbers are especially discordant in the subfamily Dicranoideae and even within the genus *Dicranum.* Partly, this disagreement can be attributed to inconsistencies among investigators in reporting the small or m-type of chromosomes. On the other hand, extra chromosomes that have long since become stabilized in a species may be of an intermediate size. For example, Bryan (l.c.) reported for several species of *Bruchia* an intermediate-sized chromosome that dissociates precociously and behaves during meiosis in a characteristic manner. These species, including *B. brevifolia, B. fusca,* and *B. texana,* are thus reported correctly to have the number n=15, whereas related species apparently have an identical complement except that they lack the intermediate precociously dividing bivalent. The number n=14 is thus correct for species of the latter group (e.g., *Bruchia ravenelii* and *B. flexuosa*).

The Japanese species of *Dicranum,* including *D. japonicum* Mitt., *D. undulatum* Hedw., *D. majus* Turn., *D. nipponense* Besch., and *D. caesium* Mitt., are consistently reported by Japanese investigators to have a haploid number of 11, while nearly all North American and European species seem to have the number n=12. A possible explanation for these inconsistencies may lie in the fact that the Japanese reports (See Yano, 1957a) are based upon somatic material obtained from gametophytic plants, while other reports (Vaarama, 1950a, Steere, 1954; Bryan, 1956a) describe meiotic divisions. Small m-chromosomes apparently cannot always be detected in somatic cells (See Bryan, 1955), and this may account for some of the differences in numbers reported for the same species.

ENCALYPTACEAE

Encalypta apophysata Nees & Hornsch.

n=13 (Fig. 38)

This is the first report of the chromosome number of this species, which in North America is restricted to the Rocky Mountains of Montana and northward. A notable cytological feature of the single population studied is the relatively small size of the SMC, at least in comparison with other species so far investigated, *E. vulgaris* var. *mutica* (Steere, Anderson & Bryan, 1954), *E. alpina, E. procera,* and *E. rhabdocarpa* (Steere, 1954) and *E. ciliata* (reported below). The size of the SMC may bear some relationship to the size of the mature spores, since the spores of *E. apophysata* are smaller than those of any of the species mentioned above, except for those of *E. procera.* Steere's drawing of *E. procera* shows quite a large SMC. This is interesting in view of the fact that he found the chromosome number to be approximately doubled, namely, n=27. A comparison of figures 38 and 39 shows a remarkable size difference between the SMC of *E. apophysata* and *E. ciliata.* The chromosomes of *E. apophysata* are uniform in size, and no meiotic irregularities were observed. As noted by Steere (1954), the cytoplasm in the SMC of all species thus far studied in the Encalyptaceae is exceedingly opaque, owing to the presence of large numbers of refractive inclusions, probably oil bodies. Although the chromosomes stain intensely with acetic orcein, they are scarcely visible through the dense opaque materials in the cytoplasm. By following the techniques worked out by Bryan (1955) for similarly filled *Sphagnum* SMC, this problem was overcome. Her technique consists of fixing the punctured capsules for longer periods of one to 48 hours. This leaves the cytoplasm clear, transparent, and usually free of stain so that a good contrast between chromosomes and cytoplasm is achieved.

Encalypta ciliata Hedw.

n=13 (Fig. 39)

The chromosomes of this species likewise have not been studied previously. They proved to be similar in number and behaviour to those of *E. apophysata.* The chromosomes are only slightly larger than in *E. apophysata,* but the SMC, as already noted, are much larger, in fact among the largest observed in the present study. Steere (1954), in reporting 14 bivalents in *E. alpina* and 27 in *E. procera,* observed one minute bivalent in each species and thought that a second minute chromosome may occur in *E. procera.* Because of optical difficulties occasioned by the densely filled cytoplasm, however, Steere felt somewhat uncertain about the numbers reported for *E. alpina* and *E. procera.*

We wish to acknowledge the kindness of Dr. Seville Flowers, who checked the determinations of all the collections of Encalyptaceae.

POTTIACEAE

Hymenostylium recurvirostrum (Hedw.) Dixon

n=13 (Fig. 40–43)

This number is the first record for any species of *Hymenostylium,* a segregate of *Gymnostomum.* It is very widely distributed in calcareous situations throughout the world and is highly variable, with at least two reasonably well-marked forms or "varieties" recognized in North America, var. *scabrum* Lindb. and var. *commutatum* (Mitt.) Hag.

Chromosomes were studied from three populations, all from Waterton Lakes National Park, and, although the number proved to be the same in all three, the meiotic chromosomes differ so remarkably in other respects that a description of each is in order. Figures 42 and 43 represent sporocytes from plants collected at Red Rock Canyon (No. 150) and exhibit rather remarkable size differences among chromosomes. There is one small bivalent; it was not observed to disjoin prematurely. Note that in figure 42 some of the larger bivalents have begun to disjoin, but the tiny bivalent is still tightly joined. Figure 40 was drawn from a population from the townsite of Waterton Lakes (No. 88); note that it does not include in its complement a small bivalent corresponding to that shown in figures 42 and 43. A third population, also from the townsite of Waterton Lakes (No. 142), differs still more. The SMC of this population (Fig. 41) are nearly twice as large as those of the other two, and the chromosomes differ also. The longer and larger bivalents are particularly noticeable. At first it was thought that these two large chromosomes might be heterochromosomes of a single bivalent, but both were observed to disjoin at anaphase and are, therefore, unquestionably bivalents.

The significance of this variation in meiotic chromosomes from different populations of apparently the same species is not known. It is difficult to compare the morphology of bivalents from various populations.

The manner in which the bivalents are joined, the number and position of chiasmata, and the centromere position are all difficult features to determine in mosses. The small chromosome size, usually coupled with the lack of diakinetic figures, contributes mainly to this difficulty. Finally, the rather firm pressures that are required to separate the usually tightly clumped moss chromosomes undoubtedly cause some distortion and further exaggerate the bivalent configurations.

Hymenostylium has been segregated from *Gymnostomum* primarily on the basis of its stylostegous capsules, i.e., capsules in which the operculum remains attached to the columella after dehiscence and finally falls with it. It is also characterized by triangular stems lacking a central strand, whereas the stems of *Gymnostomum* are rounded and have a small, more or less distinct central strand. Andrews (1943) reported that the shape of the stem as seen in section and even the absence of a central strand are subject to variation in *Hymenostylium recurvirostrum,* and Loeske (1910) pointed out that stylostegy occurs in many species of quite diverse relationships and often in species obviously and intimately related to non-stylostegous ones, as in *Desmatodon, Pottia,* and *Tortula,* and stylostegy is therefore not in itself a just reason for generic segregation. Cytological information on *Gymnostomum calcareum* and *G. aeruginosum* and also on *Eucladium verticillatum* should be helpful in determining the relationships of *Hymenostylium* and its value as a segregate from *Gymnostomum.* One recent author, Jensen (1939), has quite logically included all the species mentioned above, together with *Hymenostylium recurvirostrum,* in the genus *Eucladium.* We feel that *Hymenostylium* and *Gymnostomum* are best combined, and certainly *Eucladium* is not far distant from *Hymenostylium,* in gametophytic characters at least. The fact that *Hymenostylium, Gymnostomum,* and *Eucladium* all occupy similar very wet and highly calcareous habitats and thus have similar ecological requirements may also indicate a degree of relationship, in view of their other similarities.

Tortella tortuosa (Turn.) Limpr.

n=13 (Fig. 44, 45)

This genus is another for which no previous chromosome counts are known, although nearly 40 species have been described. The SMC of this species are the smallest encountered in the present study and must be among the smallest in mosses. As can be seen in figures 44 and 45, they are only one-third to one-fourth the diameter of most moss SMC. The mature spores in this collection are 8 to 9.5 μ in diameter and thus, though small, are not unique among mosses. The chromosomes are also small, but they stain brilliantly with acetic orcein and are among the easiest to prepare for study that we have examined. Three bivalents tend to disjoin before the others, as can be seen in figure 44, a side view of MI. During prometaphase and early metaphase the bivalents are extremely condensed, as shown in figure 45. This stage is of considerable duration, for in almost every preparation numerous sporocytes were observed with the chromosomes in this condition. Meiosis proceeds almost simultaneously in the SMC of a single capsule.

Bryoerythrophyllum recurvirostrum (Hedw.) Chen

n=13 (Fig. 46, 47)

Four populations of this common and widespread species were investigated. All were found to have 13 clear and unmistakable bivalents, thus agreeing with the number reported by Steere (1954). A characteristic large bivalent seen by Steere in Alaskan material was also observed in all the Rocky Mountain collections studied (Fig. 46). This large bivalent disjoins first and may explain Steere's observation that "occasionally another large bivalent appears." In figure 47, the two disjoined half-bivalents can be seen lying some distance apart in the drawing, which is a polar view of an early MI. The other bivalents have not yet started to separate. Steere reports the large bivalent as being dimorphic, but we have been unable to confirm this.

Though commonly included in *Didymodon,* this species belongs to a fairly sizable group of species characterized by relatively broad, often dentate leaves with enlarged, lax, thin-walled, and transparent cells in the basal portion and by capsules which (in some instances, if not all) dehisce by means of an annulus. Information on the cytology of species of *Didymodon,* in a more restricted sense, should be very instructive, not only in placing the relationships of *Bryoerythrophyllum* but also in clarifying the confused concepts of *Barbula* and *Didymodon* currently presented in the literature.

Pottia heimii (Hedw.) Fürnr.

n=26 (Fig. 48)

This count confirms a previous report by Steere (1954), who observed 26 bivalents in an Alaskan population. Our drawing (Fig. 48) matches his illustration almost exactly, including the presence of one small bivalent and at least five bivalents with terminal centromeres and sub-median chiasmata. Chromosome numbers are known in three additional species of *Pottia*: *P. davalianum,* n=30 (Steere, *et al.,* 1954); *P. truncata,* n=25 (Vaarama, 1950a); and *P. obtusifolia,* n=50 (Steere, 1954). It is curious to find such diverse chromosome numbers in a genus most of whose species appear to be morphologically closely allied.

Steere (1954) referred to *Pottia heimii* as an "essentially maritime species of boreal regions." Dixon (1924) reported that in England it is one of the few distinctly maritime mosses but is also found inland, and Nyholm (1956) said that it is widespread on sea shores in Scandinavia and rarely found inland. In North America, however, Wareham (in Grout, 1928–40) gave the habitat more realistically, it seems, as "usually on moist alkaline and saline soils, frequently a sea coast plant," and the range as New Mexico, Colorado, Utah, Wyoming, Montana, Idaho, Alberta, and Ontario, all inland, and also Newfoundland, Greenland, the west shore of Hudson Bay, and St. Paul and St. Matthew Islands in the Bering Sea, all supposedly maritime. These records and a number of other more recent inland collections indicate that *Pottia heimii* is perhaps edaphically restricted to alkaline situations but not at all limited to the halophytic environments of sea-coasts. The collection used in this study came from a muddy ledge of a cliff at the upper falls of Beauty Creek in Jasper National Park, a calcareous but not saline habitat.

Stegonia latifolia (Schwaegr.) Vent.

n=26 (Fig. 49, 50)

The count recorded here is the first report of the chromosome number of this exceedingly rare and interesting species. Although only a single population was investigated, a generous quantity of capsules was available for study, and numerous preparations were made. By comparing figures 49 and 50 of *S. latifolia* with figure 48 of *Pottia heimii*, a close similarity can be seen in the number, size, and appearance of the chromosomes. Both species possess 25 comparatively large bivalents plus one small bivalent, which in *S. latifolia* becomes greatly attenuated and stretched following application of pressure on the SMC. Both figures 49 and 50 show this feature to advantage. The relatively small size of the chromosomes as compared with the large size of the SMC is another characteristic shared by both species.

It is perhaps strange that the chromosomal resemblances between *S. latifolia* and the species of *Pottia* thus far investigated (particularly *P. heimii*) are so great. *Stegonia latifolia* and its var. *pilifera* are often included in *Pottia*, since the sporophytes are very similar, but the peristome is better developed in *Stegonia* than in any of the American species of *Pottia*, and the gametophyte is quite unlike that of any other *Pottia*. The curious bulbiform habit of growth, the odd leaf outline, and the smooth, rhomboidal leaf cells are quite distinctive and seem to us to warrant recognition on the generic level.

The junior author has collected *Stegonia latifolia* only a few times, in the Yukon and the Rocky Mountains, but he has made dozens of collections of the var. *pilifera*, there and at Churchill, Manitoba. He has collected the two together only twice and has never seen evidence of the intergradation which many European authors mention. The presence of a hyaline hair point in the variety may not, in fact, justify any taxonomic rank higher than a variety. Data on the cytology of the variety might provide a certain answer to whether it should be elevated in rank, as we suspect it should.

Desmatodom latifolius (Hedw.) Brid.

n=26 (Fig. 51, 52)

At least four populations of this moss were studied, and all were found to have 26 bivalents. There is a strong tendency for early or prometaphase chromosomes to clump, and considerable care was necessary to obtain good preparations. When too much pressure is applied, many bivalents exhibit long, attenuated, thread-like extensions (Fig. 52). Occasional side-view MI figures were obtained in which the chromosomes were spread out without the application of much pressure, and chromosomes of such figures (Fig. 51) lack the long attenuations visible in figure 52.

This investigation is the first of the chromosomes of *D. latifolius*. Steere, Anderson, and Bryan (1954) found 13 haploid chromosomes in *D. hendersonii*, while Steere (1954) reported 25 bivalents in *D. cernuus*. The presence of 13 chromosomes in *D. hendersonii* may give evidence that

D. latifolius and *D. cernuus* are tetraploids. It must be pointed out, however, that the relationships of these species are obscure. *Desmatodon,* as generally understood in North America, is a highly synthetic genus. Although *D. latifolius* and *D. cernuus* show considerable similarities and very likely belong in the same genus, *D. hendersoni* is quite different. It greatly resembles *Didymodon tophaceus* and seems to have been separated from *Didymodon* and placed even less convincingly in *Desmatodon* on the basis of its costal structure. Both *D. hendersoni* of western American distribution and *D. sprengelii* of Florida and the American tropics are quite unrelated to the majority of species included in *Desmatodon* in Grout's *Moss Flora.*

Tortula mucronifolia Schwaegr.

n=12, n=24 (Fig. 53–55)

Two populations of this moss were studied, one from Kicking Horse Canyon in Yoho National Park with the number n=12; the other from Johnson Canyon in Banff National Park, found to be tetraploid, with the number n=24. Both numbers, furthermore, are at variance with Steere's (1954) report of the number n=30 for an Alaskan population of the same species. It should be noted that Steere experienced difficulty in "distinguishing between bivalent and univalent chromosomes at metaphase I" and expressed doubt concerning the number which he reported. In any case, a possible basic number of six is suggested.

No special difficulties were experienced, however, in interpreting material from either population studied here, for excellent preparations were obtained from both. From the Kicking Horse Canyon plants we observed sporocytes in late diakinesis and early MI (Fig. 53), so that the problem of precocious separation of bivalents did not interfere with the count. Figures 54 and 55 are polar and side views, respectively, of MI stages; the latter reveals especially well the bivalent nature of the 24 chromosomes of the tetraploid population. The 13 bivalents of the diploid population were observed in several capsules and presented no particular problem in interpretation (Fig. 53). A comparison of figure 53 with both figures 54 and 55 shows that the SMC of the diploid population are about one-half the diameter of those of the tetraploid population. Mature spores from diploid plants measured 11 to 16 μ in diameter as compared to 14 to 20 μ in the tetraploid. A study was made of the morphological features of plants from both diploid and tetraploid populations, especially as to robustness of plants, size and shape of leaves, and size and density of papillae on the leaf cells. No differences were observed in any of these respects. The slight differences in spore size between the diploid and tetraploid populations are probably insignificant.

Other instances of intraspecific chromosome populations in the genus *Tortula* have been reported. Steere, Anderson, and Bryan (1954) found the numbers n=12, n=25, and n=36 in three different Californian populations of *T. princeps,* while Vaarama (1953a) reported for *T. muralis,* also from California, n=48, n=60, and n=66. Other numbers reported for this genus are n=13 for *T. bolanderi;* n=12 and n=15 for *T. laevipila;* n=49 for *T. subulata* (Steere, Anderson & Bryan, 1954; Vaarama, 1953a); and n=12 for *T. ruralis* (see below). This large and unwieldy genus consists of more than 225 species. Thus many more species must be studied before conclusions can be made concerning the basic chromosome number or correlations between chromosomes and taxonomic sections. At present, polyploid populations with haploid numbers of 12, 24, and 36 in *T. princeps* and the numbers 48, 60, and 66 in *T. muralis,* suggest that six may possibly be the basic number, and Steere's report of the number n=30 in *T. mucronifolia* supports this notion. In a genus with widespread polyploidy and aneuploidy the question will not be settled easily.

Tortula ruralis (Hedw.) Smith

n=12 (Fig. 56, 57)

Tortula ruralis is locally very common, as it is in most parts of North America and Europe. It is surprising, therefore, that there have been no previous chromosome counts for it. The species is quite variable, but the plants used for cytological study were fairly typical in development and unquestionably belong to *T. ruralis.*

A single population was studied, and only one capsule was found with dividing sporocytes, but the one preparation yielded such convincing figures that the count is reported with confidence. Slight size differences are seen among the 12 bivalents, and one disjoins early so that late metaphase I figures often show 13 chromosomes; two, however, are half-bivalents, as can be seen in figure 57. The haploid number, 13, is encountered in so many of the Pottiaceae, and especially in the genus *Tortula,* that the number n=12 in *T. ruralis* seems noteworthy.

Chromosome counts have been made in only two of the four subfamilies of Pottiaceae. Some apparent differences of interest are suggested by the following summary:

Subfamily Pleuroweisioideae

Subfamily Merceyoideae

Subfamily Trichostomoideae
Astomum, n=13, 26
Weissia, n=13, 14
Timmiella, n=14
Tortella, n=13
Bryoerythrophyllum, n=13
Barbula, n=10, 11, 12, 13, 14

Subfamily Pottioideae
Acaulon, n=26
Phascum, n=26, 28, 52
Pottia, n=25, 26, 30, 50
Stegonia, n=26
Desmatodon, n=25, 26
Aloina, n=23, 28
Tortula, n=12, 13, 15, 24, 30, 36, 40, 48, 49, 50, 55, 60, 66

One is immediately struck with the high incidence of polyploidy in the Pottioideae as compared with the Trichostomoideae, in which, except for a single species of *Acaulon,* there are only aneuploid differences. The basis for the separation of these two subfamilies resides essentially in the presence of both dorsal and ventral stereid bands in the costa of the Trichostomoideae, while in the Pottioideae there is only a single, dorsal stereid band. Also in the latter the leaves are mostly broad and tend to be ovate, lingulate, or spatulate in contrast to the more narrowly lanceolate leaves of the Trichostomoideae. Neither of these characters suggests an especial relationship with the polyploid situation in the Pottioideae, although it is perhaps true that in this subfamily there is a tendency for larger cells. Of more significance, however, is the fact that nearly all the members of the Trichostomoideae are dioicous, whereas a high proportion of the genera of the Pottioideae are monoicous (and often synoicous). The correlation between synoicous inflorescence and diploid gametophyte has been repeatedly emphasized (Heitz, 1942; Lowry, 1948, 1954a; Yano, 1957a, b. c.), although there are notable exceptions (see *Dicranum fuscescens,* above). Yano (l.c.) has reported identifying both X and Y chromosomes in presumed diploid gametophytes of numerous species. Wettstein (1937, 1940) was able to produce experimentally tetraploid sporophytes of *Bryum caespiticium;* spores from these sporophytes grew into diploid and synoicous, rather than haploid and dioicous gametophytes.

It will be most rewarding, indeed, when chromosome counts are obtained for the subfamily Pleuroweisioideae, which differ remarkably from the other members of the family in having lateral rather than terminal sporophytes. North American representatives of this family (*Anoectangium* and *Molendoa*) rarely produce capsules.

GRIMMIACEAE

Grimmia affinis Hornsch

n=13 (Fig. 58)

This is apparently the first report of the chromosome number of this species, which is quite common in the mountains and in northerly latitudes in North America. Two populations were investigated, both with 13 bivalents. The SMC are among the smallest yet seen in the genus *Grimmia,* but the meiotic chromosomes are easily counted at MI. They stain intensely and spread apart easily. The chromosomes are uniform in size except for a single slightly larger bivalent.

The nomenclatural history of the species is quite involved. We have followed Sayre (1951) in rejecting the name *G. ovalis,* which was misrepresented in Grout's *Moss Flora* and consequently misused by most American authors. *Grimmia affinis* is supposed to be autoicous, but the presence of both male and female buds on the same plants is often very difficult to demonstrate. Although most of the stems of plants reported here had only female inflorescences, a few were found with male buds as well. (Dr. Geneva Sayre kindly confirmed the determinations of these plants.)

Grimmia affinis and *G. montana* (see below) are obviously congeneric and were placed by Brotherus (1924–25) and others in the subgenus Guembelia. They are only distantly related to the other species of *Grimmia* that we have investigated and that many authors assign to the genus *Schistidium.*

Grimmia alpicola Hedw.

n=13 (Fig. 59, 60)

Four populations of this complex species were investigated. All the material examined presented problems of interpretation, but we are of the opinion that the haploid chromosome number is 13. Whether each chromosome is a bivalent or univalent is very difficult to determine. Also disjunction occurs at such irregular rates that anaphase I figures are confusing. Figure 59 is a side view of metaphase I, showing nine bivalents aligned across the metaphase plate, while four bivalents have already disjoined. The four half-bivalents of the latter can be seen in anaphase. Numerous side-view metaphase I figures, similar to that drawn in figure 60, were observed. Twelve distinct bivalents can be seen across the plate, whereas two half-bivalents are at anaphase.

Grimmia alpicola var. *latifolia* (Zett.) C.M.

n=13 (Fig. 61, 62)

Steere (1954) investigated a population of this arctic and alpine variety from Alaska and concluded that the haploid chromosome number is 14, a number previously unreported in *Grimmia.* In fact, largely on the basis of the chromosome number, Steere accorded specific recognition to the plants and applied to them the name *G. platyphylla* Mitt.

We examined material of this variety from two populations in the Rocky Mountains, and in both we found the number n=13. Chromosome behaviour in the var. *latifolia* and *G. alpicola* is strikingly different. The bivalents in var. *latifolia* all disjoin at about the same time, thus presenting no problem in the recognition of bivalents. Also, the chromosomes are little or not at all stretched in late metaphase and early anaphase while the bivalents are separating, a condition which was observed in *G. alpicola.* A comparison of figure 59 (*G. alpicola*) with figure 61 (var. *latifolia*) emphasizes the differences in chromosome appearance at disjunction. In addition, the chromosomes of *G. alpicola* tend to clump badly at all stages, but especially at MI, while those of var. *latifolia* show little or no tendency to clump. The significance of these differences in reflecting relationship, however, is not clear and must await additional study. The effects of environmental influences on the appearance and behaviour of meiotic chromosomes are especially in need of study.

Sayre (1952) reduced both the var. *latifolia* and the var. *rivularis* to the synonymy of *G. alpicola* and furthermore considered the latter a mere variety of *G. apocarpa.* It must be admitted that *G. apocarpa* and *G. alpicola* are related and that both are so enormously variable that they and their numerous forms and varieties are exceedingly difficult to understand. We do not know the reasons leading Sayre to her conservative viewpoint, but we feel strongly that combining all the variants of a large and puzzling complex does not solve the problems but actually creates new ones. A very good example of this was provided by Dixon's treatment of

Sematophyllum caespitosum (Dixon, 1920). Because he found considerable variation and overlapping of characters, he combined a very large number of species from tropical regions all over the world, with the result that it is impossible at present to develop any kind of specific concept of *Sematophyllum caespitosum* or to separate it from most of the other species of the genus!

We do not understand *Grimmia apocarpa* or *G. alpicola* well enough to suggest a final answer to the problem, but we believe that a more practical solution would be to keep the two separate until much more ecological and cytological evidence is available and that in spite of its intergradations toward *G. alpicola* var. *alpicola* on the one hand and into var. *latifolia* on the other, the var. *rivularis* should be maintained. Although we think that the variation and intergradation are too great for var. *latifolia* to stand as a species in its own right, we agree with Steere that geographically and morphologically it would seem to be a genetic entity. We would continue to treat it as a variety. The cytological reasons which Steere gave for recognizing the var. *latifolia* as a species are not convincing inasmuch as his count of 14 chromosomes does not agree with ours, n=13, a number which we also found in *Grimmia alpicola* var. *alpicola*. Even if 14 is the correct number in the Alaskan material, its significance is not clear since 10, 12, 13, 14, and *ca.* 20 chromosomes have been reported for *Grimmia apocarpa* (Ho, 1956; Vaarama, 1953a; Steere, Anderson & Bryan, 1954; Anderson & Bryan, unpublished; Heitz, 1928), and therefore chromosome numbers alone apparently will not help in elucidating relationships within the *G. alpicola-apocarpa* complex. (A thorough review of opinions in the literature concerning this complex is given by Loeske, 1913, pp. 41–44.)

Grimmia apocarpa var. *pulvinata* (Hedw.) Jones

n=14 (Fig. 63)

A confusing series of chromosome numbers has been reported for the difficult *G. apocarpa* complex. Chromosome counts include n=12, for a Finnish population (Vaarama, 1953a); n=13 for two Californian (Steere, Anderson & Bryan, 1954) and one French population (Ho, 1956); n=14 for several populations in North Carolina (Anderson & Bryan, unpublished); and an earlier count by Heitz (1928), who reported the number n=*ca.* 20.

Quite likely two chromosome races of *G. apocarpa* occur in North America, with haploid numbers of 13 and 14, respectively. On the other hand, some interpretation is required in arriving at either number, for most preparations contain figures which could be interpreted either as 13 or 14. It is necessary to rely almost entirely upon MI figures for purposes of counting, for in anaphase I there appears to be a tendency for the separating half-bivalents to break up prematurely into their respective sister chromatids. Because of the small size, it is not always possible to distinguish between sister chromatids and half-bivalents. Second division figures are so badly clumped that the discreteness of the chromosomes is obscured.

Metaphase I figures of *G. apocarpa* include a single large chromosome that could be interpreted either as a single bivalent or as two bivalents in juxtaposition, and the differences in numbers reported may derive from this large chromosome. Ho (1956) studied somatic tissue and concluded that 13 somatic chromosomes make up the gametophytic complement of his plants collected in France, and although problems of interpretation also occur with somatic material, this is evidence for the existence of two chromosome races.

The genus *Schistidium* has been segregated for a considerable group of species characterized by immersed, stylostegous capsules enveloped in noticeably enlarged perichaetial leaves, but exceptions even in stylostegy occur within the genus. Vilhelm (1922) has stated the case for *Schistidium* very well: "Les limites de ce genre ne sont pas, il est vrai, assez nettes, mais néanmoins les espèces que doivent y être rangées se distinguent des autres de genre *Grimmia* d'une façon frappante par leur aspect extérieur, par le forme des touffes, par celle des tiges, par l'anatomie des feuilles, par les sporogones et par leur écologie. Si nous approuvons la proche parente du genre *Schistidium* avec le genre *Grimmia* il importe peu que nous qualifions ces groupes de genre ou de sous-genre. Il est certain, que le genre *Schistidium* forme un groupe spécial d'espèces, qui se distingue parfaitement des espèces du genre *Grimmia*." Loeske (1913) maintained *Schistidium* as a genus but admitted that the limits between *Schistidium* and *Grimmia* are not at all distinct and defended his position rather lamely by saying, "Der Unterschied zwischen Gattung und Untergattung is ohnedies fast undefinierbar gering, und die Teilung is zweckmässig, wenn die Gruppe gross ist." We will agree that the species of *Schistidium* form a natural group, but we do not approve of the multiplication of genera merely for the sake of convenience. We feel that the relationship of *Schistidium* is expressed much better by retaining it as a subgenus of *Grimmia* than by granting it co-ordinate rank as a genus. Thus far we have no cytological evidence to support the segregation of *Schistidium*.

Grimmia montana BSG

$n=13$ (Fig. 64)

No previous report of the chromosomes of this species has been made. This count is based on a single capsule, which unfortunately contained only a few sporocytes in meiosis. There appears to be little question, however, that the number $n=13$ is correct. The chromosomes apparently have the same tendency to clump and adhere at MI as has been reported in some other species of *Grimmia*. Also, a single large chromosome is present in this and apparently other species. One bivalent disjoins early. The half-bivalents are indicated by arrows in figure 64. A second bivalent apparently has a single terminal chiasma, and when it disjoins, the chromosomes are drawn out into a very long thread-like connection, apparent in figure 64.

A number of species of *Grimmia* have already been studied cytologically. As has been pointed out, the puzzling and variable *Grimmia* (Schistidium) *apocarpa* complex also seems to have a variable chromosome number. In *G. apocarpa*, itself, haploid numbers of 12 (Vaarama, 1953a), 13 (Steere, *et al.*, 1954; Ho, 1956), 14 (reported here), and *ca.* 20 (Heitz, 1928), have already been reported. The closely related *G. alpicola* from the Canadian Rocky Mountains has 13, as does its var. *latifolia,* but in Alaska, Steere (1954) found the number n=14 in the latter variety. Apparently, then, variability in chromosome number occurs throughout the *G. apocarpa* complex.

Previous chromosome counts for *Grimmia* proper (exclusive of *Schistidium* and *Coscinodon*) are summarized below. The species are arranged in the *Gruppen* used in Loeske's monograph (1930):

A. Gastrogrimmia

B. Litoneurum

C. Alpestres
    G. alpestris Nees, n=13
    G. montana BSG, n=13

D. Alpinae
    G. affinis Hornsch., n=13

E. Pulvinatae
    G. pulvinata (Hedw.) Smith, n=13

F. Torquatae

G. Rhabdogrimmia
    G. trichophylla Grev., n=13, 26
    G. muehlenbeckii (Schimp.) Husn., n=14+2
    G. patens (Hedw.) BSG, n=22

It is interesting to note that *Grimmia patens* is considered by many authors to belong in *Rhacomitrium* rather than in *Grimmia.* This view is apparently supported by the chromosome number n=22, which seems an anomaly in *Grimmia.*

FUNARIACEAE

Funaria hygrometrica Hedw.

n=14 (Fig. 65)

This count is of unusual significance, because this is the first "wild" population of *F. hygrometrica* in North America in which the haploid number, n=14, has been observed. The European population of *F. hygrometrica,* from which Wettstein (1923, 1924) obtained his remarkable series of tetraploid and hexaploid races through regeneration of sporophytes, had the number n=14. All previous studies of populations from so-called "natural" habitats in North America revealed the number n=28. This fact led Steere, Anderson, and Bryan (1954) and later Vaarama (1955) to speculate that weedy greenhouse populations might represent a race distinct from those growing as a weed in nature. The present discovery, however, of a diploid population in the Rocky Mountains refutes this notion. The plants were growing in a typical habitat, intermingled with sterile *Ceratodon* and *Bryum,* on disturbed soil at Bow Lake.

SPLACHNACEAE

Splachnum ovatum Hedw.

n=9 (Fig. 66, 67)

The number n=9 agrees with that reported by Steere (1954) for *S. vasculosum,* but Schweizer (1923) observed only eight bivalents in *S. sphaericum* (a synonym of *S. ovatum*). Bornhagen (1930) reported a polyploid series of numbers, n=8, 16, and 32, in different populations of *S. ampullaceum.* Our counts are based on seven populations, collected near Lake Louise, Moraine Lake, and Lake O'Hara. All the collections were obtained in quantity, and the material was in excellent condition for cytological study. It was possible to study numerous preparations from each population, and there is therefore good reason to believe that the number is uniformly nine and that Schweizer's report of eight is in error. Additional counts in the genus may be very revealing. All the North American species seem clearly related, but *S. ovatum* is unique in having the sterile tissue at the base of the capsule differentiated as an hypophysis only slightly wider than the urn, whereas in all the other species the hypophysis is conspicuously wider than the urn. *Splachnum ovatum* resembles *Tetraplodon mnioides* in this respect, and although they should not be confused, they are probably closely related.

The chromosomes of *S. ovatum* do not stain readily in acetic orcein, and it is necessary to allow the sporocytes to remain in contact with an excess of dye for several hours in order to stain them satisfactorily. The chromosomes are remarkably uniform in size except for one bivalent which is slightly smaller and stains somewhat more lightly than the others. A similar chromosome was noted by Steere (1954) in *S. vasculosum.*

BRYACEAE

Pohlia cruda (Hedw.) Lindb.

n=10+4, n=40 (Fig. 68–71)

This first reported instance of a high polyploid number in the genus *Pohlia* is not surprising in view of the high incidence of polyploidy in the allied genus *Bryum,* where haploid numbers of from 10 to 50 have been reported. Steere (1954) has previously recorded the number n=10 for *P. cruda,* based on an Alaskan population, but made no mention of the presence of small m-chromosomes. In the Rocky Mountain collection made near Kicking Horse Canyon, at least four pairs of small m-chromosomes were observed in addition to 10 large bivalents. The m-chromosomes are in nearly all respects identical with those described for *Sphagnum* by Bryan (1955). She was able to demonstrate constancy in the number and behaviour of m-chromosomes among different populations of the same species and often differences in number and behaviour from species to species. As in *Sphagnum,* the m-chromosomes stain faintly. Their behaviour could not be followed in detail, but the number appears to be constant from one plant to another. In figure 70, the four m-bivalents have disjoined, although three are still connected by tiny, barely-discernible threads. These fine connecting threads were commonly but not always observed between separating half-bivalents. Not infrequently a quadripartite m-chromosome, as shown in figure 71, was observed; it is the result of the separation of the four chromatids of the original bivalent to form an open square in which the four chromatids are at the corners, each connected by tiny threads. Bryan (1955) observed identical behaviour in Sphagnum. Other m-bivalents in this population of *P. cruda* apparently disjoin into four chromatids with no visible connecting threads (Fig. 71). Thus, prometaphase SMC of *P. cruda* exhibit perplexing and often confusing variation in the number of small chromosomes, depending on the progress and extent of disjunction of the m-bivalents. As few as four and as many as 14 small chromosomes were observed, but in all instances they could be accounted for as precociously separated chromosomes from the original four m-bivalents.

A second population of *P. cruda*, collected at Sentinel Pass above Moraine Lake proved to have the high polyploid number $n=40$ (Fig. 68 and 69). Three capsules of this population were studied in meiosis, and none exhibited m-bivalents, in spite of careful observations. The SMC of the polyploid population are notably larger, as can be seen by a comparison of figures 70 (from the diploid population) and 69 (from the octoploid population). Figure 68 was drawn from an SMC of the latter population, which had been broken open by excess pressure, so that the bivalents were well spread apart and easily counted. No m-bivalents were observed in this and other similarly ruptured SMC, so that it must be concluded that the m-chromosomes are absent in the high polyploid population.

Yano (1953) studied the somatic chromosomes of four species of *Pohlia* from Japan and found two dioicous species, *P. fauriei* and *P. elongata*, to be diploid, having the number $n=11$ $(10+1)$, while the two monoicous species, *P. elongata* and *P. longicollis*, were tetraploid, with the number $n=22$ $(20+2)$. In a later report (1957a), Yano listed the chromosome numbers of 10 additional species of *Pohlia*, seven of which are dioicous and three monoicous. Again, all of the dioicous species are diploids ($n=10$, 11), while the three monoicous species are tetraploids ($n=20$, 22). In the dioicous, diploid species, Yano observed two heteropycnotic chromosomes, one large and one small, and described the complement as follows: $n=10=V(H)+2J+6(2v+4j)+m(h)$ or $n=11=V(H)+2J+7(2v+5j)+m(h)$. By the same token, according to Yano, the monoicous tetraploid species have the complement $n=20=2V(H)+4J+12(4v+4j)+m(h)$ or $n=22=2V(H)+4J+14(4v+10j)+m(h)$. It should be pointed out, however, that Yano's identification of the smallest and largest chromosomes of the complement with the two heteropycnotic chromosomes observed in non-dividing nuclei is based purely on the assumptive generalization that the smallest and largest chromosomes of the moss complement are always heteropycnotic. It has not been established that this is always the case in mosses, although both Heitz (1928) and Yano (1951, *et seq.*) have shown it to be true in a few instances, notably in *Mnium* and in the Polytrichaceae. Whether the m-bivalents observed at meiosis and nearly always negatively heteropycnotic correspond to the heteropycnotic chromosomes observed in the somatic cells of gametophytic tissues is also not established. More extensive observations along these lines are needed before much weight can be accorded Yano's generalizations. The behaviour of the heteropycnotic elements through the meiotic cycle should be especially studied.

It is also of some interest that Yano (1957a) found the haploid number 11 in *Pohlia wahlenbergii*, which is often placed in the genus *Mniobryum*. The karyotype of *P. wahlenbergii* was found to be identical with that of other dioicous species, including *P. scabridens* (Mitt.) Broth., *P. revolvens* (Card.) Nog., *P. columbica* (Kindb.) Broth., *P. carnea* (Hedw.) Lindb., *P. acuminata* Hoppe & Hornsch., *P. suzukii* Ochi, *P. nutans* (Hedw.) Lindb., and *P. patentissima* Ochi.

The somatic chromosomes of *P. cruda* have apparently not been investigated.

Leptobryum pyriforme (Hedw.) Schimp.

n=20 (Fig. 72, 73)

Surprisingly, this cosmopolitan and often weedy species, which produces sporophytes in great abundance, has not been investigated cytologically before now. There is a cytological resemblance to the species of *Bryum* in both number and appearance of chromosomes. The characteristic large bivalent is also present in *L. pyriforme*. In both figures 72 and 73 it can be seen standing out in strong contrast to the other smaller bivalents. The latter, incidentally, are remarkably uniform in size and configuration. Since the number n=20 is a tetraploid number for the family (in terms of the sporophyte) it is significant to note that only a single large bivalent is present in the complement of *L. pyriforme*. The possibility, therefore, of the present population having arisen from recent autopolyploidy seems unlikely. Only a single population was studied. Observations on additional populations will be of interest to see whether diploids of this rather variable species exist. The cytological similarity between *Leptobryum* and *Bryum* is interesting, since *Leptobryum* belongs in the subfamily Pohlioideae and *Bryum* in the Bryoideae, according to Andrews (in Grout, 1928–40), and gametophytically the two genera do not seem very closely related.

Bryum pseudotriquetrum (Hedw.) Schwaegr.

n=20 (Fig. 74)

Two previous counts of this very widespread and variable species resulted in the numbers n=9–10, (Heitz, 1928) and n=11 (10+1) (Steere, Anderson & Bryan, 1954) in populations from Germany and California, respectively. The lowest number yet found in the genus *Bryum* is 10 (n). Both aneuploidy and polyploidy have occurred during speciation, for the numbers n=11, 12, and 13, as well as the numbers n=20, 30, 40, and even 50 (Steere, 1954) have been observed in "wild" populations. Aneuploidy may (Steere, Anderson & Bryan, 1954) or may not (Steere, 1954) involve the small chromosome. Various numbers have been reported for *Bryum argenteum*, the weedy and ubiquitous species commonly known as the "silvery Bryum." Marchal (1920), Jachimsky (1935), and Yano (1956) all found a haploid number of 10, but Steere (1954) reported the number n=11, while Steere, Anderson, and Bryan (1954) found that n=12.

The latter investigators found, in addition to 10 large chromosomes, one or two small chromosomes. In *B. capillare,* another exceedingly common and widespread species, there are five small bivalents in addition to the regular 10 large bivalents characteristic of the genus (Steere, *et al.,* 1954).

No small bivalents are present in *B. pseudotriquetrum* from the Rocky Mountains, at least in the single population studied. It is clearly a tetraploid. The absence of small bivalents indicates that the ancestral diploid (or diploids) either lacked a small bivalent or, if present, the one or two bivalents that would be expected in an allo- or autotetraploid have since been lost. Unfortunately Wettstein's (1937) original strain of *B. caespiticium,* from which through sporophytic regeneration he was able to obtain an octoploid race (n=40, 2n=80), contained in its complement only the 10 large bivalents apparently basic to the genus. It would be most illuminating to induce polyploidy beginning with a strain which has, in addition to the 10 large bivalents, one or more pairs of small chromosomes and to observe their behaviour and stability in the higher polyploids.

In the population of *B. pseudotriquetrum* studied here, meiosis appears to be normal. No multivalents, excessive lagging of chromosomes, or chromatin bridges were observed.

Andrews, in his masterful and realistic treatment of the genus *Bryum* (in Grout, 1928–40), included *B. bimum* and *B. pseudotriquetrum* in a single species, because he found that they "do not differ apart from the inflorescence, and this at times varies even in the same tuft." Traditionally the name *B. bimum* has applied to synoicous plants and *B. pseudotriquetrum* to dioicous ones. Holmen (1953) has expressed the opinion that *B. pseudotriquetrum* and other "good old species" should not have been included in *B. bimum.* Persson (1952) also protested that "even if two forms differ only in one distinct character . . . but have different distribution areas (as *B. bimum–B. pseudotriquetrum* and *Lophocolea bicuspidata–L. cuspidata*), we ignore nature in including one of the species as a synonym of the other." Neither author gave any constructive suggestions for a better understanding of the species involved, and they provide no information on the North American distributions of dioicous and synoicous forms of the complex. We have no opinion on the subject, but we feel confident in referring our material to B. *pseudotriquetrum* because the plants are dioicous.

Bryum pendulum (Hornsch.) Schimp.

n=10 (Fig. 75)

No previous counts are known for this species. The number n=10 coincides with the basic number (at least as considered at present) for the genus and possibly the family. In several species of *Bryum,* a single larger and more conspicuous bivalent has been observed (Steere, Anderson & Bryan, 1954; Steere, 1954; Yano, 1950, *et seq.*). Yano considered this larger bivalent to be the sex chromosome and contended that it is heteropycnotic. In *B. pendulum,* however, the large bivalent is not so noticeable as in some species of *Bryum,* because at least three other bivalents of the complement are almost as large. The smallest bivalent disjoins precociously, but in all other respects meiosis is regular. It is worthy of note that, as in the following species, the plants are synoicous, although the chromosome number indicates that the gametophytes are haploid. (That the basic number for *Bryum* is five, instead of 10, is still a possibility.)

?Bryum turbinatum (Hedw.) Schwaegr.

n=10+1 (Fig. 76).

We were unable to identify this collection with certainty, and Dr. A. Le Roy Andrews suggested that it might be *B. turbinatum*. The plants are synoicous, however, rather than dioicous, as *B. turbinatum* should be.

In spite of the uncertain identification, the results are included here because of the striking and distinctive chromosome complement observed. Also, the SMC are apparently the largest that have yet been observed in the genus, not excepting a 50-chromosome (n) population of an unnamed *Bryum* from Alaska (Steere, 1954). The chromosomes of the present population are large and distinctive. At least two bivalents have an O-configuration suggestive of median centromeres and two terminal chiasmata; at least two other bivalents have subterminal centromeres with single terminal chiasmata (Fig. 76). In the latter category are a medium-sized, prematurely dissociating bivalent and the large bivalent characteristic of the genus *Bryum*. The large bivalent, however, does not disjoin early as in *B. pendulum*. In addition to the 10 large bivalents, a single small bivalent was observed in all SMC studied. The small bivalent stains intensely. It separates precociously into two half-bivalents (Fig. 76) which are in late anaphase or early telophase before the 10 regular bivalents start to disjoin in MI.

On the basis of our present knowledge of chromosomes in the genus *Bryum*, this number would indicate a sporophytically diploid species, although, as previously noted, the possibility of finding a species with the haploid number n=5 still exists. It is significant, however, that this collection is synoicous, a fact not in agreement with the often expressed generalization that haploid gametophytes are correlated with unisexual and diploid gametophytes with bisexual inflorescences. The only natural polyploids yet reported for *Bryum* have been the five species in Alaska studied by Steere (1954). Unfortunately he did not record the sexual conditions in those polyploid populations, but three of the species in question, *B. arcticum* (R.Br.) BSG, *B. inclinatum* (Web. & Mohr) Sturm, and *B. nitidulum* Lindb., are normally synoicous, and *B. calophyllum* R.Br. is autoicous; the fifth species was unidentified.

MNIACEAE

Mnium serratum Brid.

n=12 (Fig. 77, 78)

This appears to be the first investigation of the meiotic chromosomes of this species. Lowry (1948) described the somatic chromosomes from gametophytic tissues of a Michigan population. He reported 12 chromosomes (n=12) which could be classified into six pairs, the members of each pair being the same length. The spindle-fibre attachment regions were not determined, however.

The meiotic chromosomes are large and distinctive and stain exceedingly well with acetic orcein. Meiosis is regular, and the bivalents separate at about equal rates. Figure 78 is a drawing from a SMC in late anaphase II, showing 12 chromosomes at each of the four poles. Two chromosomes have been displaced from one of the groups through pressure in preparation. Although it is not possible to pair off the bivalents into six groups, as Lowry did with somatic chromosomes, the presence of two noticeably large and two noticeably smaller bivalents is obvious. (The great condensation of the chromosomes in meiosis prevents identifying the intermediate bivalents on the basis of length.) As in other 6- and 12-chromosome species of *Mnium*, there is no minute early-disjoining chromosome or chromosomes.

Mnium spinulosum BSG

n=8 (Fig. 79)

The number n=8 has already been reported for this species by Lowry (1948), but this is the first investigation of meiotic chromosomes. Three populations (two from Montana and one from Jasper National Park) were studied, all having eight bivalents. A single large bivalent, longer and considerably thicker than the others, is the last of the set to disjoin. Furthermore, at least one of the half-bivalents tends to lag behind the others, as shown in Figure 79. The bivalent doubtless corresponds to the long chromosome with a terminal attachment region described by Lowry (1948) in the somatic complement. As is evident in Figure 79, the long-lagging half-bivalent has a terminal attachment region. We can confirm Lowry's observation that all the other members of the complement have median or sub-median attachments.

As in the previous species, the SMC undergo distinct interkinesis following the first or heterotypic division. The two daughter nuclei apparently remain in this condition for some time, as numerous capsules were examined in which the SMC were in this stage. Anaphase I chromosomes of *Mnium* are long and somatic-like, as are the second division chromosomes, resembling in this respect such meiotic chromosomes as those of *Lilium* and *Tulipa*.

This is the only 8-chromosome *Mnium* known to date, and the chromosome number of some 28 species and varieties of the genus has been investigated. The numbers n=6, n=12, n=7, and n=14 have also been reported. Lowry (1948) has postulated several interesting modes of origin for the 8-chromosome condition.

MEESIACEAE

Meesia uliginosa Hedw.

n=13 (Fig. 80, 81)

No previous count is known for this large and distinctive moss, although Steere (1954) reported the number n=10 for another member of the genus, *M. triquetra*. The difference in chromosome number is not entirely unexpected, because, gametophytically, the species differ conspicuously in structure and appearance. In fact the arrangement of the leaves and their shape in *M. triquetra* are so strongly suggestive of *Paludella* that one wonders why *M. triquetra* has traditionally been bound to *Meesia* rather than segregated as a genus or perhaps included in *Paludella*. Chromosome studies of *Paludella* should be highly instructive.

Steere (1954) encountered difficulties in obtaining satisfactory preparations of both *M. triquetra* and *M. uliginosa*. He found the cytoplasm of the SMC filled with oil droplets, which obscured the chromosomes to such an extent that he was unable to approximate a count in the latter species. We found that these difficulties could be mostly overcome by the use of a longer fixation period, from 10 to 30 minutes or even longer. Also, by applying a firm, even, and rather heavy pressure on the cover glass after the chromosomes were well stained, most of the opaque materials could be squeezed out of the SMC. In this way we were able to obtain a cell which was optically almost clear. The chromosomes absorb the dye slowly and are thus inclined to stain rather faintly. It was found advisable, however, not to add additional stain after the oily substances had been pressed from the SMC. When this is done, the cytoplasm takes up the dye rapidly, thus lessening the differential staining between chromosomes and cytoplasm.

The meiotic chromosomes of *M. uliginosa* are large and exhibit little variation in size. A few of the bivalents are distinctive in morphology (Fig. 81). The attachment regions appear to be mostly terminal (Fig. 80), although at least four chromosomes have median or submedian centromeres. Judging from Steere's (1954) description, as well as his figures of *M. triquetra*, the chromosomes seem quite different from those of *M. uliginosa*. He described two minute chromosomes in the complement of *M. triquetra*. In *M. uliginosa*, however, small or minute chromosomes are absent. The smallest chromosome of the complement, furthermore, disjoins last at MI and was frequently observed in AI figures to lag behind the other chromosomes in their movement to the poles. These observations furnish additional evidence for the considerable and probably fundamental distinctness of these two species.

CATOSCOPIACEAE

Catoscopium nigritum (Hedw.) Brid.

n=14 (Fig. 82, 83)

This unique moss does not seem to have been investigated cytologically until now. The meiotic chromosomes exhibit the poorest staining qualities of any moss encountered in this study. Numerous variations in technique were employed in an effort to improve the staining, but none was entirely satisfactory. Both prefixation treatments and mordants were tried with little success. Best results were obtained by long fixation, usually 12 hours or more. The columella with the surrounding sporogenous tissue was carefully dissected out so as not to rupture the spore layer and placed immediately in the fixative in a watch glass. After 12 or more hours the material was placed on a slide in a drop of fixative, and the spore layer was dissected free of the columella, which was discarded. An excess of acetic orcein was then added, the cover glass applied, and the slide placed in a covered petri plate on filter paper saturated with fixative or water to prevent evaporation of the dye. The slide was allowed to remain there for five to eight hours before the excess dye was removed, and the chromosomes were flattened with slight pressure. After ringing with vaseline, the slide was stored at room temperature for as long as three or four days to allow the chromosomes to take up additional stain.

Even in the best preparations, the chromosomes of *C. nigritum* appear somewhat diffuse and are often connected with fine threads. Apparently, the matrix fixes very poorly, for the chromosomes in many preparations appear somewhat reticulate. Although it was not possible to determine the configurations of the bivalents, most chromosomes appear to have terminal attachment regions (Fig. 83). In figure 82, two bivalents have already disjoined.

Catoscopium is a monotypic genus which has been included by various authors in the Meesiaceae and the Bartramiaceae. Flowers (in Grout, 1928–40) treated it as an anomalous member of the Bartramiaceae, as many older bryologists had, but others, including Brotherus (1924–25) and most recent bryologists, have placed it by itself in the monotypic Catoscopiaceae, between the Meesiaceae and the Bartramiaceae. Its relationship to the Meesiaceae is not particularly obvious but is suggested somewhat by the shape of the capsule, which is very small, smooth, and so strongly curved that the mouth is directed downward and is not at all similar to the capsules of the Bartramiaceae. The leaves are suggestive of the Bartramiaceae in shape and areolation, but the costa consisting of homogeneous cells contrasts with the highly organized costa found in the Bartramiaceae. The fact that the capsules of *Catoscopium* lack stomata (apparently present in all the Bartramiaceae) may also have some significance. But the diffuse nature of the chromosomes and their poor staining qualities remind one of the chromosomes of the Bartramiaceae, which are likewise difficult to stain and often appear to be somewhat reticulate. The chromosome numbers known for the Bartramiaceae ($n=8$, 12, and 16) are not helpful in solving the problem, but the similar reactions to fixing and staining indicate that *Catoscopium* is probably correctly placed near, but not necessarily in the Bartramiaceae.

BARTRAMIACEAE

Bartramia ithyphylla Brid.

$n=12$ (Fig. 84)

Two populations of this moss were studied cytologically, and both agree with previous counts by Vaarama (1950a) and Steere (1954). The meiotic chromosomes of *B. ithyphylla* are among the largest, if not the largest, that have been observed in mosses, even bigger than the large and distinctive bivalents in the Mniaceae. In contrast to the dark-staining chromosomes of the latter family, however, the chromosomes of *B. ithyphylla* stain lightly with both acetic orcein and acetic carmine. Moreover, the cytoplasm stains rather heavily with these dyes so that the contrast between chromosomes and cytoplasm is weak. In several SMC, metaphase chromosomes appear reticulate, probably because of the poor fixing qualities of the matrix. Diakinesis was not observed.

Yano (1957a) has described the karyotypes from somatic cells of two species of *Bartramia* from Japan, *B. crispata* Schimp., and *B. pomiformis* Hedw. Both have the number n=8, which had already been reported for *B. pomiformis* by several investigators. Vaarama (1950a) suggested that the basic chromosome number for the genus may be four, and comparisons of the morphology of the gametophytic complement by Lowry (1954) and Yano (l.c.) support Vaarama's assumption.

It is worth noting that the fixing and staining characteristics of the chromosomes in the Meesiaceae, Catoscopiaceae, and Bartramiaceae are remarkably similar.

Philonotis fontana (Hedw.) Brid.

n=6 (Fig. 85, 86)

The number n=6 agrees with Vaarama's report (1953a) on Finnish material and conforms also to Yano's report (1950) for *P. japonica*. Yano (l.c.) has also found the number n=12 for *P. socia* in Japan and more recently (1955b) has described a population of this species with the number n=6. An early report by Heitz (1928), listing the number for *P. fontana* in Germany as n=7–8, is probably incorrect. Four populations of *P. fontana* from the Rocky Mountains and one from Ontario were studied. All were found to be uniform in number.

The six bivalents are distinctive and differ rather characteristically in size and configuration (Fig. 85 and 86). One of the bivalents uniformly assumes an O-configuration at late diakinesis or prometaphase and can be recognized in every sporocyte. Another bivalent regularly disjoins prior to the first metaphase of the other bivalents (Fig. 85), a fact which may explain Heitz' count of seven chromosomes.

Of the species thus far investigated cytologically, *P. fontana*, *P. falcata* (Hook.) Mitt. (*P. carinata* Mitt.), and *P. lancifolia* Mitt. (n=6) belong in the section Euphilonotis, and *P. socia* (n=12) in Philonotula. Apparently *P. japonica* (n=6) also belongs in Philonotula, but there may be some doubt since Brotherus (1924–25) omitted reference to it, although in the first edition of his "Musci" in *Die natürlichen Pflanzenfamilien* (1893–1909) he had placed it in Philonotula.

TIMMIACEAE

Timmia austriaca Hedw.

n=16+1 (Fig. 87, 88)

The chromosome number of this species is previously unreported, but a related species, *T. cucullata*, has been investigated by Scheuber (1932), who found a haploid number of 12, and by Lowry (1948, 1953), who reported the number n=16. The present count agrees with Lowry's observations on *T. cucullata* except for the presence in *T. austriaca* of a small bivalent which disjoins early (Fig. 88). It absorbs acetic orcein readily and stains brilliantly. The 16 larger meiotic chromosomes are somewhat variable in size and at MI are considerably condensed. At least two bivalents appear somewhat larger (Fig. 87). In the latter figure, the small bivalent is shown prior to disjunction, while in figure 88 it has already disjoined, with the half bivalents in anaphase and the other bivalents still on the plate.

The morphological features of *T. cucullata* and *T. austriaca* are similar, the specific differences being that *T. cucullata* has appendiculate cilia on the endostome, hyaline or yellowish leaf bases, and costae not toothed at back and is autoicous, whereas *T. austriaca* has merely jointed cilia, orange leaf bases, and frequently toothed costae and is dioicous. The difference in sexual condition is interesting in view of the similar chromosome numbers and indicates that here also we have an example of bisexuality that is not associated with polyploidy.

ORTHOTRICHACEAE

Orthotrichum alpestre Hornsch.

n=11 (Fig. 89)

The chromosomes of this species have not been investigated previously, but the number n=11 conforms with that reported for other members of the "Orthotricha straminea" group. The complement includes one conspicuously larger chromosome and a small precocious bivalent which divides considerably sooner than the other bivalents. This precocious behaviour has been noted in other 11-chromosome species of *Orthotrichum* by Vaarama (1950a) and also by Steere, Anderson, and Bryan (1954).

Orthotrichum alpestre is very common in the Canadian Rockies. Eight populations from Banff National Park were studied; the collections were made in rather widely separated localities at Bow Lake, Baker Creek, and the Continental Divide on the Windermere Highway. In all the specimens the meiotic chromosomes were remarkably similar in appearance and behaviour.

It seems unfortunate that the sculpturing of the peristome teeth, though highly variable in this species, has been used as a primary basis for the recognition of two North American varieties, var. *occidentale* (James) Grout and var. *watsoni* (James) Grout, both said to occur in "the Rocky Mountain region" (Grout, 1946). All the Canadian material seems to belong in the species proper, in spite of some variation in the teeth. Characteristically the teeth are papillose below but irregularly papillose-striate near their tips. Actually, most often only the subterminal division of a tooth shows striae at all clearly and there only as short, irregular lines or ridges oriented more or less vertically among the papillae which are present there also. The striae are weak at best, and often scarcely discernible; occasionally the teeth are nearly smooth at the tips. Sometimes on the same capsule, teeth may be papillose throughout, while others are more or less striate. Such differences in degree of sculpturing seem to be subject to non-genetic factors and are perhaps associated with the stage of development. A young capsule may not have developed the full expression of striation, or a very old one may have suffered from erosion. We suspect, on the basis of material available, that these two varieties are no more than forms which do not deserve the dignity of varietal rank.

Orthotrichum rupestre Schleich.

n=6 (Fig. 90)

This species was reported by Steere, Anderson, and Bryan (1954) to have a haploid number of six, based on a collection from Yosemite National Park, California. Our material from Sunwapta Falls, Jasper National Park, is thus confirmatory. As in the Californian population, the Rocky Mountain material exhibited one large, somewhat elongated chromosome. Although the present count is based on a single capsule, there is no question concerning the number. All of the 6-chromosome species of *Orthotrichum* investigated to date are exceptionally easy to count and include some of the most favourable cytological material among the mosses.

Orthotrichum jamesianum Sull.

n=18 (Fig. 91, 92)

The chromosome number of this species differs so strikingly from previous counts in the genus *Orthotrichum*, that the first populations studied were erroneously thought to belong to *Ulota*, an allied genus with rather high chromosome numbers. The characters of *O. jamesianum*, however, are so distinctive that the species can be recognized in the field after only casual examination, and there is no question of its relationship to *Orthotrichum*. Reliable counts were made on at least seven populations, from Banff, Kootenay, and Waterton Lakes National parks, and all proved to have the number n=18.

In the complement of *O. jamesianum*, one large pair of chromosomes tends to disjoin precociously in many sporocytes (Fig. 92), but not in all. A small chromosome pair, however, does disjoin early with complete regularity (Fig. 92). In figure 91 the complement is figured at early MI, before either of the aforementioned bivalents has started to disjoin.

Of the many species of *Orthotrichum* for which chromosome counts are available, those with superficial stomata have the number n=6, while those with sunken stomata have all been reported to have the number n=11, except for the present species and *O. stramineum*, a 13-chromosome species (Vaarama, 1953a).

Orthotrichum jamesianum is very common and widely distributed in the Canadian Rocky Mountains, both in British Columbia and Alberta. It is probably common in the mountains southward as well, although it has been reported only from Nevada where the original collection was made in the East Humboldt Mountains.

Although the chromosome counts are at variance with all other counts of *Orthotricha* with immersed stomata, there are no structural peculiarities either of the gametophytes or the sporophytes unless it be the absence of an endostome, a negative character which scarcely justifies challenging the position of the species in *Orthotrichum*. This species is sufficiently similar to *O. alpestre* to make Grout's sketchy treatment (1946) of the two rather confusing, but it is clearly distinct in a number of characteristics and not at all likely to be mistaken for *O. alpestre*. The absence of an endostome and the fact that the peristome teeth are clearly striate throughout (rather than faintly striolate above) are enough to distinguish *O. jamesianum* from *O. alpestre,* and, in addition, the plants are so distinctive in aspect that they can be recognized in the field without a lens. The tufts are short and compact, with a dull, red-brown or dark coloration throughout, and seem invariably rather sandy, dirty, or even slightly mouldy, and the leaves are closely appressed when dry, whereas *O. alpestre* is looser, with leaves spreading and somewhat contorted when dry, and the tufts are pale green above and not noticeably dull or dirty in normal appearance. The regularly forked papillae on the leaf cells of *O. alpestre* are also distinctive.

Orthotrichum laevigatum Zett.

n=6 (Fig. 93)

Four populations of this species were investigated, and all were found to have the number n=6, agreeing with the number reported by Steere, Anderson and Bryan (1954) from a California population. In all the Rocky Mountain populations, the smallest bivalent was observed to disjoin early only occasionally. It is customary in most 6-chromosome species for the smallest bivalent to disjoin precociously (see Vaarama, 1953; Steere, Anderson & Bryan, 1954).

Another feature of meiosis in this species is the fact that it occurs before the SMC can be freed from the columella with ease. In previous *Orthotricha* studied, the SMC float away from the columella as soon as dissected from the capsule. In *O. laevigatum,* however, the post-meiotic tetrad condition is reached before the sporocytes behave in this manner.

Orthotrichum roellii Vent.

n=6 (Fig. 94, 95)

No previous reports of the chromosome number of this species are known. Typical of species with superficial stomata, the haploid number is six. Two bivalents are rather large, and three are medium-sized, while the sixth is small. An unusual feature of meiosis in *O. roellii* is that both the largest and smallest bivalents disjoin early (Fig. 94). It was possible to follow the distribution of the respective chromatids to each of the four daughter cells. Figure 95 shows a spore mother cell in late anaphase II, in which six chromosomes can be distinguished in each of the four anaphasic groups.

Orthotrichum sordidum Sull. & Lesq.

n=6 (Fig. 96, 97)

The chromosome number of this species was not known previously. Four populations from the upper peninsula of Michigan were investigated. The present count adds another 6-chromosome species to the growing list of *Orthotricha* with superficial stomata. The complement of *O. sordidum* is identical to that of the two previous species. A smaller chromosome disjoins precociously and is well into anaphase by the time the remaining large bivalents disjoin (Fig. 97). In one of the populations studied it was possible to observe very late diakinetic figures, and the configurations are shown in figure 96. One of the bivalents with median or submedian centromeres assumes a distinctive O-shaped configuration with two terminal chiasmata. Another has terminal centromeres and two chiasmata, and one bivalent also with terminal centromeres has a single chiasma.

Orthotrichum speciosum Nees

n=6 (Fig. 98)

Both Vaarama (1950a) and Steere (1954) have already reported the number n=6 for this species, and the present study confirms these counts from three additional populations. Steere found evidence of early disjunction of the largest bivalent, but our observations indicate just the opposite. The larger bivalent is usually delayed, and the half-bivalents lag somewhat behind the others during anaphase I (Fig. 98). It should be stated, however, that size differences among the four larger bivalents are not conspicuous.

This species of western distribution is very closely allied to the eastern *O. elegans*, from which it differs essentially in quantitative characteristics and in distribution. The two have been greatly confused, and it appears that no hard and fast line can be drawn between them. No cytological studies are known for *O. elegans*. *Orthotrichum speciosum* is related to a very robust species of West Coast distribution, *O. lyellii*. It is interesting that *O. lyellii*, which is dioicous, has the same chromosome number (Steere, Anderson & Bryan, 1954) as *O. speciosum*, which is monoicous (with the antheridia and archegonia in separate buds on the same plants).

Orthotrichum texanum Sull.

n=6 (Fig. 99)

This species was counted previously by Steere, Anderson, and Bryan (1954) from a Californian population, and the present study, also from a single population, confirms their report. The chromosomes of the Rocky Mountain plants are similar in all respects to other known 6-chromosome species. A late diakinetic or prometaphase figure is shown in figure 99. A comparison of this figure with figure 98, which shows a chromosome group in the same stage but from a population of *O. speciosum*, emphasizes the remarkable constance and uniformity of the meiotic chromosomes of the 6-chromosome species.

Ulota cirrata (Bernh.) Grout

n=20+2 (Fig. 100, 101)

Ulota cirrata proved to be one of the most difficult species to count in the entire study. An abundance of material was available, however, and it was fortunately possible to obtain meiotic stages from numerous capsules from two populations. Different bivalents were found to disjoin at unequal rates, resulting in an almost indistinguishable mixture of bivalents and half-bivalents. The present count was arrived at only after studies were made of numerous sporocytes at early MI and at anaphase II stages where the chromatids could be distinguished. Twenty large bivalents and two small chromosomes make up the complement. The two small bivalents disjoin early. In figure 100 both of the latter have disjoined, while in figure 101 one of the small bivalents has already disjoined into two half-bivalents, but the other has not yet divided.

Vaarama (1950a) found an n-number of 21+1 in *U. curvifolia* (a synonym of this species) and 21 (19+2) in *U. crispa;* Yano (1951) at first reported the number n=8 for *U. japonica* but later (1957c) published the count n=10, based on both somatic and meiotic divisions. Ho (1956) found 10 haploid chromosomes in gametophytes of *U. hutchinsiae.* Thus, the basic chromosome number appears to be 10, *Ulota crispa* and *U. cirrata* being tetraploids, while *U. japonica* and *U. hutchinsiae* are diploid species. It is noteworthy that the small, precociously disjoining chromosomes have been seen only in the tetraploids. Yano (1957c), in commenting on Vaarama's report of 21 bivalents plus one "accessory" chromosome for *U. curvifolia,* suggested that the accessory chromosome may have resulted from the precocious dissociation of an "m-m pairing." If the latter is true, then Vaarama's count would be 20+2, which agrees with ours.

AMBLYSTEGIACEAE

Cratoneuron falcatum (Brid.) Roth

n=7 (Fig. 102, 103)

The chromosome number of this species was reported as 10 by Yano (1952, as *C. glaucum* var. *falcatum*). He had originally reported the number for *C. filicinum* var. *japonicum* to be n=9 (1950) but later (1955) decided that it should be re-interpreted as n=10.

Excellent preparations were obtained of metaphase I chromosomes of *C. falcatum.* Meiosis apparently begins in this species at the base of the spore sac and proceeds progressively toward the tip. A single capsule can thus be found with all stages of meiosis in evidence. Chromosomes stain brilliantly with acetic orcein, and the bivalents are well spread apart at MI. Little or no pressure is required to separate the bivalents. Only a single population was studied, but the material was plentiful and in good condition.

The systematic position of *Cratoneuron* is debatable. The presence of papillae as a constant or occasional feature on the leaves of many of the species and also of paraphyllia on the stems is suggestive of *Helodium* and thus the Thuidiaceae. On the other hand, considerable resemblance to species of *Drepanocladus* and *Hygroamblystegium* give witness to a natural affinity with the Amblystegiaceae as well. Loeske (1910) suggested that *Cratoneuron, Hygroamblystegium,* and *"Thuidium"* (in a very inclusive sense) developed in different lines from an ancestral group of a general *Thuidium*-like nature. We feel that morphologically *Cratoneuron* falls quite naturally into the Amblystegiaceae and that the relationships between that family and the Thuidiaceae are such that no distinct boundary can be expected to occur between them. The chromosome number reported here, n=7, is apparently unique in the Amblystegiaceae. Previous numbers found in that family are as follows: *Campylium*, 9, 20, 22 (Yano, 1950; Steere, 1954); *Leptodictyum*, 10, 24 (Yano, 1953; Ho, 1956); *Amblystegium*, 12, 20, and 22 (in natural populations) (Steere, *et al.*, 1954; Vaarama, 1950a, 1953a, 1956) and 24 and 48 (in races produced artificially through apospory by Marchal, 1912, and by Wettstein, 1924); *Hygroamblystegium*, 12, 20 (Steere, *et al.*, 1954; Marchal, 1912); *Drepanocladus*, 12, 22 (Vaarama, 1950a, 1953a; Steere, 1954; Steere, *et al.*, 1954); and *Hygrohypnum*, 10 (Vaarama, 1956). Furthermore, the chromosomes of *Cratoneuron falcatum* are not especially suggestive of other members of the Amblystegiaceae. They are larger, more condensed and show no signs of stickiness. Cytological information from both families, and particularly from *Helodium* and *Drepanocladus* will doubtless help to place *Cratoneuron* more naturally in the taxonomic system.

Loeske (1910) studied carefully the ecology and taxonomy of *Cratoneuron* in Europe, and since the North American species are mostly the same as the European, his comments are pertinent to the present study. He found that the well-developed papillae regularly found on the leaf cells of *Cratoneuron decipiens* can also be found to a greater or lesser degree on occasional specimens of all other European species, with the exception of *C. irrigatum*. The only European species free of intergradations in important structural features is *C. decipiens*, and, according to Loeske, it is the only "good" species of the genus. All the others could logically be included in *C. commutatum* because of their obvious relationships and complete intergradations one with the other. Loeske gave a very interesting and detailed account of those variations and the obvious influence of environment on them, and presented, in fact, a good case for considering them mere ecological expressions of *C. commutatum*. To refer to such ecotypes as forms or races rather than some higher taxonomic categories implying genetic differentiation seems more realistic to us. Loeske preferred, however, to retain the specific categories rather than to dismiss the problem by "lumping" all the variants into one species of immense variability. From our rather limited experience with the problem and our difficulty in finding limits between *C. commutatum* and *C. falcatum* in North America, we feel that *C. falcatum* ought to be degraded at least to a varietal status under *C. commutatum;* many European authors have already treated it in this way.

Amblystegium juratzkanum Schimp.

$n=12+1$ (Fig. 104)

This species and the next were found, growing intermingled, in a collection from the upper peninsula of Michigan. Both bore capsules in meiotic condition. The number $n=12+1$ was likewise found by Steere, Anderson, and Bryan (1954) for a Californian population of *A. juratzkanum*. Both the Californian and Michigan populations possess, in addition to the 12 large bivalents, a small bivalent which disjoins prematurely, although in the Michigan material it apparently does not disjoin as early as observations on California plants indicated. Figure 104 shows the small bivalent before disjunction.

The Marchals (1911, 1912) and Wettstein (1924) found a chromosome number of 12 in the related species *A. serpens* and produced experimentally through sporophytic regeneration a polyploid series of strains with the numbers n=24 and n=48. They did not describe a small bivalent. In the light of these numbers, it is curious that Vaarama (1950, 1953a) should find the number n=22 in two widely separated populations from Finland and California. The species of *Amblystegium* are, however, not well understood and are notoriously polymorphic. It is likely that much of the variation is associated with environmental differences, but there must be at least some differences that are genetically controlled.

Amblystegium varium (Hedw.) Lindb.

n=12+1 (Fig. 105, 106)

Curiously enough, this common and widespread species has not previously been studied cytologically. The meiotic chromosomes of our collection from northern Michigan differ scarcely from the previous species except in a greater tendency for the small bivalent to dissociate early. The several large and distinctive chromosomes can be matched almost exactly in the two species.

This species provides a close link between the other members of *Amblystegium* and the segregate *Hygroamblystegium* currently in favour. Grout (1909) granted *Hygroamblystegium* only subgeneric rank and found *A. varium* to be intermediate in nature, but more closely allied to the subgenus Hygroamblystegium than to Euamblystegium. Loeske (1910) also considered this matter carefully and agreed that Hygroamblystegium should not be granted independent status. In his more recent treatment, however, Grout (1928–40), perhaps influenced by contemporary European authors, reversed his position by recognizing *Hygroamblystegium* and excluding from it *Amblystegium varium*! We believe that his original concepts were nearer the truth. It is perhaps significant that numbers already reported for *Hygroamblystegium*, n=12 and 20, are the same as those known for *Amblystegium*. Another genus which is essentially a segregate of *Amblystegium* (but probably of diverse origin) is *Leptodictyum*, in which the numbers n=12 and 24 have been found.

Campylium stellatum (Hedw.) Lange & C. Jens.

n=18+2 (Fig. 107, 108)

The number reported here differs from the 6 to 8 recorded by Heitz (1928) and the 22 by Steere (1954), but, in any case, the North American populations appear to be polyploids in terms of the European number. Possibly the discrepancy between our Rocky Mountain count and Steere's Alaskan report is due to differences in interpretation of the small bivalents, although the possibility of chromosome races also exists. Certainly the species is remarkably variable throughout its very wide range of distribution.

Although the numbers do not coincide, the general appearance, character, and sizes of the chromosomes of *Campylium* compare favourably with those of *Amblystegium*. (Compare, e.g., fig. 107, 108 with fig. 104-106.) Chromosomes of *Campylium* are relatively smaller but possess the same order of size variations.

Campylium, as currently understood in Europe and North America, is an inclusive genus and, in Loeske's opinion (1910), a very artificial one. His provocative discussion of nearly 50 years ago still warrants serious consideration, and it will be interesting to see if his opinions will eventually be supported by cytological evidence. He believed that *Campylium* should be restricted to the *C. halleri-hispidulum-sommerfeltii* group, while *C. chrysophyllum, C. stellatum, C. polygamum*, etc. should be put into *Chrysohypnum*, where he would also include *Leptodictyum riparium* because of its close similarity to *Campylium polygamum*. Such a disposition seems to us, superficially at least, quite defensible. The relationship of *C. halleri, C. hispidulum*, and *C. sommerfeltii* to the Hypnaceae, rather than the Amblystegiaceae, might be indicated by further cytological investigations, and such studies might also show the value of the monotypic genus *Campylophyllum* to which Brotherus (1924–25) assigned *C. halleri*.

Drepanocladus uncinatus (Hedw.) Warnst.

n=12, n=20 (Fig. 109-111)

Five populations were investigated. Four of them had the number n=20, but a single population from Cameron Lake in Waterton Lakes National Park was found to have n=12, a number which agrees with previous reports by Vaarama (1950) and Steere (1954). It is significant, therefore, to discover that the majority of the Rocky Mountain populations studied have the number n=20. In each of the two races the complements consist of large, distinctive bivalents that stain intensely with acetic orcein. Bivalents of the m-type were not observed, and there was no evidence of precocious separation among any of the bivalents. Meiosis is completely regular in the 12-chromosome race, but in the 20-chromosome race multiple association of bivalents was observed (Fig. 109). Four groups of four bivalents each occur in nearly all early or prometaphase cells, leaving four bivalents which show no tendency to group with other bivalents. The bivalents are, however, grouped together so tightly in some sporocytes as to obscure the outline of the individual bivalents that make up the groups. Figure 109 is a drawing of a sporocyte with this type of association. Note the four groups of four bivalents each and the four single bivalents, which together comprise the complement of 20 bivalents. Prior to metaphase I the secondary association breaks up, and the chromosomes become oriented on the metaphase plate as individual bivalents (Fig. 110). Disjunction appears to occur regularly, with an equal distribution of chromosomes to the four daughter cells.

All the specimens studied belong to the same form of the species, and we could see no correlation between morphology of plants and chromosome number.

The four species of this taxonomically difficult genus which have been investigated thus far all differ in chromosome number: *D. exannulatus*, n=12 (Vaarama, 1953a); *D. fluitans*, n=22 (Vaarama, 1953a), n=24 (Yano, 1957b); *D. revolvens*, n=23 (Steere, 1954); and *D. uncinatus*, as reported here, n=12, n=20.

The genus *Drepanocladus* is extremely difficult for the taxonomist, because nearly all its species are complexes of numerous extremely variable forms. It is entirely possible that the genus is actually a convenient repository, a "pigeon-hole," for poorly understood species of diverse origin. Loeske (1910), for example, thought that *Drepanocladus uncinatus* differs in origin from the *D. aduncus* group so greatly that, phylogenetically, entire genera and even families separate them. We do not have sufficient evidence at the moment to challenge the traditional position of *D. uncinatus* in this genus, but it may be worth noting that Loeske believed *Ptilium* and, through it, *Ctenidium* to be rather closely related to *Drepanocladus uncinatus*. This suggestion is shocking at first, since both *Ptilium* and *Ctenidium* have such a time-honoured position in the Hypnaceae and are so frequently included in the genus *Hypnum* that one rarely thinks of the obvious resemblances of *Ptilium* to *Drepanocladus* and the Amblystegiaceae.

Hygrohypnum luridum fo. *julaceum* (BSG) C. Jens.

n=10+1 (Fig. 112, 113)

The genus *Hygrohypnum* does not seem to have received previous attention, cytologically. Two populations were studied, both of which have been assigned to fo. *julaceum* (BSG) C. Jens.

The material from Kimpton Creek in Kootenay National Park was in especially fine condition for meiotic studies, and numerous preparations were obtained from which counts could easily be made. A few sporophytes had SMC in diakinesis, and ten large bivalents plus a small bivalent, which in some diakinetic figures had already disjoined, were easily distinguished. At first it was thought that only distance conjugation occurred, but later figures were observed in which the two homologues were in close association (Fig. 112). Figure 113 shows an early metaphase figure in which the small bivalent has disjoined, but the half-bivalents are only a short distance apart. Unlike the behaviour in most mosses of precociously disjoining small bivalents, the half-bivalents remain a short distance apart until the larger bivalents disjoin and begin anaphasic separation. At this time the small half-bivalents enter anaphase, and division proceeds normally.

PLAGIOTHECIACEAE

Plagiothecium denticulatum (Hedw.) BSG

n=25 (Fig. 114–116)

This species has one of the highest numbers yet recorded among pleurocarpous species and is obviously highly polyploid, for Vaarama (1950a) found the number n=10 in a Finnish population. In spite of the high number in the Rocky Mountain population, meiosis is without apparent irregularity. No multivalents or other aberrant behaviour were observed.

The SMC are comparatively small. The meiotic chromosomes are uniform in size. They stain readily in acetic orcein and are easily spread, exhibiting little or no tendency to clump at metaphase. The SMC of

P. denticulatum separate easily from the columella at the time of meiosis. In the preceding family, the Amblystegiaceae, the SMC are not free from the original mother walls until the spores have formed.

HYPNACEAE

Hypnum cupressiforme Hedw.

n=16 (Fig. 117–119)

No previous North American populations of this exceedingly variable species have been investigated. Judging from previous counts based on European material, the North American plants investigated are probably polyploid. Chamberlain (unpublished; pers. comm. from P. W. Richards) has made an exhaustive study of the cytology, taxonomy, and ecology of this species in England. Of the rather numerous "varieties" currently recognized, he obtained chromosome counts from five, all of which have the number n=8. On this basis our material would clearly be tetraploid. Vaarama (1950a), however, reported the number n=10 for a Finnish population. Ten is a commonly found number in the Hypnaceae; Yano has reported also for *H. lindbergii* (1953), *H. fujiyami* (1952, 1955a), *H. plumaeforme* (1952, 1955a), and *H. pratense* (1952). Three species reported by Yano recently (1957b) have numbers other than 10, namely, *H. Dieckii* Ren. & Card., n=6; *H. oldhami* (Mitt.) Jaeg., n=7; and *H. reptile* Mx., n=11.

Only one population from the Rocky Mountains was studied. As can be seen in figure 117, two larger, four medium-sized, and eight smaller bivalents can be distinguished in the complement. In Vaarama's figure (1950, p. 251), three large bivalents are pictured, in addition to three medium-sized and four smaller ones. It would thus appear that there are distinctive cytological races with chromosome complements differing in both number and morphology.

Hypnum revolutum (Mitt.) Lindb.

n=14 (Fig. 120, 121)

No previous counts are known for *H. revolutum,* and the number n=14 stands in striking contrast to the numbers known for other species of this large genus of no doubt polyphyletic origin.

As in *H. cupressiforme,* two larger bivalents stand out in the complement, and there are found medium-sized bivalents that correspond approximately with those observed in *H. cupressiforme.* However, in *H. revolutum,* only six smaller bivalents were found instead of eight as in *H. cupressiforme.*

The discovery of both aneuploidy and polyploidy in the genus *Hypnum* is of considerable interest, for bryologists have not been in complete accord in their attempts to subdivide the genus into more natural segregates. The rather striking cytological differences among the species already investigated give promise that further cytological study will help in solving at least some of the problems.

A summary of the chromosome numbers reported to date for the genera of Hypnaceae, grouped according to Brotherus' treatment (1924), is of some interest in this regard.

Subfamily Pylaisioideae
- *Pylaisia,* n=11 (Vaarama, 1953a; Steere, 1954)
- *Homomallium,* n=12 (Vaarama, 1953a)

Subfamily Hypnoideae
- *Hypnum,* n=6, 7, 8, 10, 11, 14 (Yano, 1955a; Vaarama, 1950a)
- *Breidleria,* n=10 (Yano, 1953)
- *Isopterygium,* n=11, 22 (Vaarama, 1950a)
- *Ctenidium,* n=7 (Sinoir, 1952)
- *Ptilium,* n=10, 11, 10+1 (Kurita, 1937, 1939; Yano, 1952; Vaarama, 1950a)

Still too few genera and too few species have been investigated to permit us to draw conclusions, but careful comparisons of karyotypes and observations concerning chromosome behaviour may yet help in the subdivision of genera. Aneuploidy apparently has played a major role in speciation within the Hypnaceae, with obvious polyploidy apparent in only a single genus, namely, *Isopterygium,* which is discussed below.

Isopterygium pulchellum (Hedw.) Jaeg.

n=11, n=22 (Fig. 122–125)

The two populations investigated proved to be diploid and tetraploid, respectively. No previous information on the chromosomes of this species is available, but a related species, *I. turfaceum,* was found by Vaarama (1950a) to have the number n=11.

It is significant that the SMC of the tetraploid population are approximately twice the size of those of the diploid population. Figure 125 is from the tetraploid, while figures 122 to 124 are from the diploid. The chromosomes of both populations exhibit some tendency to cohere. Occasional figures were observed in which the bivalents were connected by thin threads (Fig. 122). In the diploid, two bivalents usually disjoin early (Fig. 122, 124); they include the largest bivalent in the complement and a medium-sized bivalent. In the tetraploid, disjunction is more uniform. A single small bivalent could be identified in the diploid population in sporocytes from more than one capsule (more obvious in fig. 122), but in the tetraploid at least three bivalents of this size class could be distinguished (Fig. 125). Meiosis in the tetraploid is completely regular, in so far as could be observed, with no indications of multivalent associations, lagging chromatin bridges, or other evidences of meiotic irregularities.

Unfortunately voucher specimen No. 115 contains few plants, and adequate comparisons between it and the tetraploid plants in No. 32 could not be made. With the few plants available, however, no significant differences, either quantitative or qualitative, could be detected. Mature spores of the tetraploid plants were found to be 9 to 13 μ in diameter;

spores of the diploid seemed to be very nearly mature and were mostly about 8 μ, with a few as much as 11 μ. It seems likely, therefore, that on complete maturity the spores of the diploid would be essentially the same as those of the tetraploid, in spite of the relative sizes of SMC noted above. *Isopterygium pulchellum* is supposed to be dioicous. No antheridia were found in either collection, and so it could not be determined whether bisexuality has accompanied polyploidy in this case. In this connection it should be noted that *I. turfaceum*, with the apparently basic complement of 11 chromosomes, is bisexual (autoicous).

Isopterygium is usually assigned by contemporary authors to the Hypnaceae, but many others (including Grout, 1928–40) deny it generic rank and include it as a subgenus of *Plagiothecium* and thereby shift it into an entirely different family, the Plagiotheciaceae. The generic limits are not very clearly defined, and some species presently included in *Isopterygium* are indeed related to *Plagiothecium*. The great bulk of species of *Isopterygium* seems quite naturally placed in the Hypnaceae. Not enough cytological studies have been made in either genus to permit further speculation at the present time. The numbers n=5 and n=25 have been found in *Plagiothecium denticulatum* (see above), but that species is at most only distantly related to *Isopterygium*.

Ptilium crista-castrensis (Hedw.) DeNot.

n=10+1, 2n=20 (Fig. 126–129)

We investigated both somatic and meiotic chromosomes in this attractive and familiar species. The discrepancy between meiotic and mitotic counts results from the absence in mitotic figures of the small chromosomes which are evident in meiotic metaphase figures. Both Kurita (1937, 1939) and Yano (1952) observed the number n=10 in somatic cells of the gametophyte of *P. crista-castrensis*, while Vaarama (1950a), studying meiotic material, reported the number n=11 (10+1).

Our observations are in agreement with those of all three investigators. At meiotic metaphases 10 large bivalents and a smaller bivalent which divides early are apparent. In figure 128, the 10 large bivalents are oriented on the metaphase plate, while the smaller bivalent is in the process of disjoining. The latter has disjoined in figure 129, so that 10 large bivalents and two half-bivalents can be seen in polar view. The small bivalent stains intensely with acetic orcein and is not so small as the usual m-bivalent. It differs from the regular bivalents only in that it regularly disjoins early. Vaarama (1950) has applied the term "special bivalent" to include the larger, intensely staining bivalents which dissociate early and are heteropycnotic and heterochromatic.

The somatic chromosomes of *P. crista-castrensis* were studied in young capsules during the late premeiotic divisions of sporogenous tissue. In this tissue mitosis proceeds almost simultaneously throughout the spore sac, so that it is possible to find capsules in which nearly every cell of the sporogenous tissue is in metaphase. In polar view metaphase figures 20 chromosomes are apparent (Fig. 126, 127). The chromosomes are spread apart and tend to be little or not at all clumped. Considerable variation was observed in the width and length of the chromosomes, and they can be assigned to several size classes. The larger chromosomes apparent in meiotic figures can be more or less paired off visually with the larger chromosomes in somatic figures. The somatic chromosomes in the premeiotic figure shown in figures 119 and 120, especially figure 119, are more condensed than they are in earlier divisions and, to some extent, resemble meiotic chromosomes.

No evidence could be found in any of the somatic cells of the two chromosomes equivalent to the small precocious bivalent seen in meiosis. Hundreds of somatic cells were studied in an effort to correlate the somatic count with the meiotic, but only 20 somatic chromosomes could be found in each cell. It must be concluded, therefore, that the somatic chromosomes corresponding to the small bivalent do not stain with the dyes employed in the present study.

There is evidence in the literature that a similar behaviour is found in other mosses. Bryan (1955), for example, has already pointed out that m-chromosomes observed in meiotic cells of various species of *Sphagnum* were not apparent in corresponding somatic cells of the same species. In *S. tabulare,* for instance, she found 19 large bivalents at meiotic metaphase plus two m-bivalents; in gametophytic squashes of the same species, however, only 19 chromosomes could be counted. Kurita (1939) found six somatic chromosomes in gametophytic tissues of both *Mnium trichomanes* and *M. microphyllum.* Later, however, Tatuno (1951), investigating meiotic material of both species, found, in addition to six large bivalents, a small precociously dividing bivalent and reported the number n=7 (6+1). Apparently the latter type of small bivalent is similar to the one described here and in *Ptilium crista-castrensis.*

POLYTRICHACEAE

Pogonatum alpinum (Hedw.) Röhl.

n=7 (Fig. 130)

All the species of *Pogonatum* investigated up to now have been found to have a haploid number of seven. The present species, whose number was previously reported by Steere (1954), is no exception, and our count from a single Rocky Mountain population confirms Steere's report. It is curious that tetraploid species have been reported in *Atrichum* (Lowry, 1954a) and *Polytrichum* (Kurita, 1937; Vaarama, 1953a), but not in *Pogonatum,* although about 14 species have thus far been investigated. *Pogonatum alpinum* varies considerably, in matters of size and degree of development, and many forms and varieties have been recognized particularly in the northern part of the range. The present count was taken from plants reasonably typical in development.

The systematic position of *Pogonatum alpinum* is highly debatable, and it is disappointing to find that, although quite a number of species and genera of the Polytrichaceae have been studied cytologically, the chromosome numbers thus far found in *Polytrichum* and *Pogonatum* give no information immediately applicable to the problem. Frye (in Grout, 1928–40) and other American bryologists have assigned this species to

Pogonatum, for the reason, perhaps too obvious, that it has a cylindrical capsule rather than the four-angled type eminently characteristic of *Polytrichum*. On the other hand, most European authors, including Brotherus (1924–25), place the species in *Polytrichum* section "Polytricha alpina," a rather strange assemblage of species, some with angled capsules (e.g., *P. gracile*) and some without. The species of "Polytricha alpina" have little more in common than their anomalous position in either *Pogonatum* or *Polytrichum*. They resemble species of *Polytrichum* in having stomatose capsules, but differ from both *Polytrichum* and *Pogonatum* in the absence of central thin spots on their exothecial cells. This problem must apparently be solved morphologically, and it will require a great deal more investigation than we have been able to give it, but we suspect that the species with cylindrical capsules, such as *P. alpinum* and its close relatives, should be included in *Pogonatum* as a special section and that the remainder should be retained in a corresponding section of *Polytrichum*.

A curious feature which we observed is a noticeable variation in size of the sporocytes even within the same capsule. At first we suspected that tetraploid sectors might be present, but this was soon found not to be the case. Large SMC, sometimes twice the diameter of other SMC, were found to possess seven bivalents, as did the smaller cells. The significance of these size differences is obscure. No mature spores could be found in the collection under investigation. A series of specimens from various widely separated localities from California to Nova Scotia failed to show any striking size differences in the spores.

Pogonatum alpinum var. *septentrionale* (Röhl.) Brid.

n=7 (Fig. 131)

Our observations confirm those of Steere (1954), who reported the number n=7 for the same variety collected in Alaska. The meiotic chromosomes of *Pogonatum* do not stain readily with acetic orcein, a fact which may be related to the thick sporogenous layer which is characteristic of all members of the Nematodonteae and makes it difficult to spread the SMC in a single layer.

This is an arctic and alpine expression of *P. alpinum*. The plants are small, and the capsules are also small and quite unlike those typical of the species. From the specimens available to us, it is not at all clear what the differences between var. *septentrionale* and var. *brevifolium* (R. Br.) Brid. might be, and we are not convinced that the curious plants investigated here are not worthy of a higher systematic rank; we have seen no evidence locally of the intergradation of typical *P. alpinum* into this small form, as suggested by many authors. (In Grout's *Moss Flora* the var. *brevifolium* seems to represent only a stunted growth form, with relatively short leaves. This form is very common in the North and does not seem to us synonymous with the var. *septentrionale*.)

Polytrichum juniperinum Hedw.

n=7 (Fig. 132)

This very common and widespread species has been studied by at least five previous workers. Allen (1912), Heitz (1928), Kurita (1937), Vaarama (1950a), and Yano (1953a) have reported the number n=7, or 2n=14. Our report, based on two Rocky Mountain populations, confirms those findings and adds another example of the remarkable stability and uniformity of the chromosomes of the Polytrichaceae, already pointed out by Steere (1954).

Polytrichum piliferum Hedw.

n=7 (Fig. 133)

Except for an early and possibly erroneous report of a haploid number of six (Vandendries, 1912), all investigators have found the number n=7 in this species (Heitz, 1928; Vaarama, 1950a; Yano, 1953a). Ours is the first observation of the chromosomes of a North American population. Yano (1953a) described a sex chromosome for *P. piliferum*. He considered the largest bivalent of the complement a heterochromosome which acts as a sex-determiner, designated as an X-chromosome in female plants and as a Y-chromosome in male plants. Size differences between X and Y chromosomes are slight. Although we did not examine somatic material, we were unable to identify a heterochromosome in the Rocky Mountain plants.

Polytrichadelphus lyallii Mitt.

n=7 (Fig. 134, 135)

This is the first report of the chromosome number for any member of *Polytrichadelphus*. The genus is abundantly represented in the Andes of South America and in New Zealand, Australia, and neighbouring islands, but only one species occurs in North America, and it is confined to the West. The discovery of the number n=7 is not at all surprising in view of the obvious relationship of this genus to *Polytrichum* and *Pogonatum*. The fundamental generic character for *Polytrichadelphus* is to be found in the curious form of the capsule which is somewhat laterally compressed and clearly two-ridged on the upper side and rounded (or indistinctly two-ridged) on the lower side.

Excellent diakinetic figures were observed, and one of them is shown in figure 134. Although the identity of each member of the diakinetic pair is obscure, the configurations are distinctive, and individual bivalents can be identified from cell to cell on the basis of length and width. Metaphase chromosomes are longer and thinner, and the change in chromosome shape between diakinesis and metaphase I is quite remarkable. Compare, for example, figures 134 and 135; the latter is a polar view of an MI figure.

SUMMARY

Meiotic chromosomes were counted in 146 populations of mosses, nearly all from the Canadian Rocky Mountains. Chromosome numbers established for 62 species, three varieties, and one form (distributed in 19 families and 43 genera) are listed in Table I; 29 species, one variety, and one form not previously investigated cytologically are marked with an asterisk (*). The chromosomes of one family, the Catoscopiaceae, and six genera, *Hymenostylium, Tortella, Stegonia, Catoscopium, Hygrohypnum,* and *Polytrichadelphus,* are reported for the first time.

Intraspecific polyploid races were found in *Distichium capillaceum* (n=14, 28), *Dicranum fuscescens* (n=12, 24), *Tortula mucronifolia* (n=12, 24), *Drepanocladus uncinatus* (n=10, 20), and *Isopterygium pulchellum* (n=11, 22). Little correlation between polyploidy and bisexuality was noted, and no clear evidence of other morphological variation associated with increased chromosome numbers was observed.

An intraspecific aneuploid race was found in *Pohlia cruda.*

Nearly all the species investigated have one or more small bivalents that disjoin precociously during meiosis. By the time the larger bivalents are separating at metaphase I, the small bivalents are usually in middle or late anaphase I. In a few species the half-bivalents or dyads separate into individual chromatids before metaphase II.

Secondary association was observed in the chromosome complement of a polyploid race of *Drepanocladus uncinatus.* This was the only example of unusual or aberrant chromosome behaviour noted in any of the polyploid species or races.

Recognizable patterns of chromosome number and behaviour are now apparent in some genera and families. Differences in chromosome behaviour are noticeable in the Ditrichaceae and the Dicranaceae, and in the latter family aneuploidy seems to be the rule (as thus far known, n=11, 12, 13, 14, 15, 16, 24). In the Pottiaceae, haploid numbers of 13 and 26 are most frequently encountered. The basic number for the Bartramiaceae is n=6, and all members of that family have chromosomes which are large and weak-staining in both acetic orcein and acetic carmine. Similar staining reactions may indicate a close degree of relationship between the Bartramiaceae and the Catoscopiaceae. The number n=7 (or 14) now seems firmly established for the Polytrichaceae. Previous counts in the many interrelated families of Isobryales have indicated a preponderance of species with haploid numbers of 10 or 11. We have found numerous exceptions with numbers of 7, 10+2, 12+2, 14, 16, 18+2, 20, and 25.

Nearly all species of *Grimmia* have 13 bivalents, but 14 were found in *G. apocarpa* var. *pulvinata.*

The number n=18 was found in *Orthotrichum jamesianum,* which is thus an anomaly (cytologically but *not* morphologically) among the 11-chromosome species with immersed stomata; all the species with superficial stomata studied had six chromosomes.

TABLE 1. SUMMARY OF CHROMOSOME NUMBERS

Species and Source	Ref. No.	Chromosome No.	Illustrations
FISSIDENTACEAE			
**Fissidens bryoides* Hedw.			
Between Waterton Lakes and Alderson L., Waterton Lakes Nat. Park.......	124	n=10	1, 2
	126	n=10	3, 4
DITRICHACEAE			
Ceratodon purpureus (Hedw.) Brid.			
Between Waterton Lakes and Bertha L., Waterton Lakes Nat. Park.......	111	n=13	5, 6
Distichium capillaceum (Hedw.) BSG			
Carthew Lakes, Waterton Lakes Nat. Park..............................	108	n=14	7, 8
Bow R., near Banff, Banff Nat. Park...	4	n=28	9–11
Sunwapta R., 9 mi. N. of Columbia Ice Field Chalet, Jasper Nat. Park.......	26	n=28	12, 13
DICRANACEAE			
Dicranella crispa (Hedw.) Schimp.			
Cameron Falls, Waterton Lakes Nat. Park..............................	122	n=14	14, 15
**Dicranella subulata* (Hedw.) Schimp.			
Between Waterton Lakes and Alderson L., Waterton Lakes Nat. Park.......	152	n=14+1	16, 17
	125a	n=14+1	18
	125	n=14+1	19–21
Amphidium lapponicum Schimp.			
Continental Divide on Windermere Hwy., Banff Nat. Park..............	11	n=16	22
	129	n=16	–
Cynodontium strumiferum (Hedw.) DeNot.			
Continental Divide on Windermere Hwy., Banff Nat. Park..............	145	n=14	23–25
	130	n=14	–
Dicranoweisia crispula (Hedw.) Lindb.			
L. Louise, Banff Nat. Park............	69	n=11	26
Sunwapta Falls, Jasper Nat. Park......	67	n=11	27
Oncophorus virens (Hedw.) Brid.			
Near Jasper on Yellowhead Rd., Jasper Nat. Park.........................	8	n=14	28
**Dicranum fuscescens* Turn.			
Near Jasper on Yellowhead Rd., Jasper Nat. Park.........................	87	n=12	–
	7	n=12	29
Mt. Eisenhower, Banff Nat. Park......	127	n=12	–
Sunwapta Falls, Jasper Nat. Park......	74	n=12	–
Maligne Canyon, Jasper Nat. Park.....	21	n=12	–

Species and Source	Ref. No.	Chromosome No.	Illustrations
Mt. Burgess, Yoho Nat. Park	42	n = 12	30
Baker Cr., Banff Nat. Park	94	n = 12	–
	98	n = 24	31, 32
Peyto L., Banff Nat. Park	119	n = 12	33, 34
Cameron L., Waterton Lakes Nat. Park	91	n = 12	–
**Dicranum groenlandicum* Brid.			
Medicine L., Jasper Nat. Park	15	n = 12	35, 36
**Dicranum strictum* Schleich.			
Cameron L., Waterton Lakes Nat. Park	117	n = 12+2	37
ENCALYPTACEAE			
**Encalypta apophysata* Nees & Hornsch.			
Athabasca Glacier, Jasper Nat. Park	24	n = 13	38
**Encalypta ciliata* Hedw.			
Cameron L., Waterton Lakes Nat. Park.	148	n = 13	39
POTTIACEAE			
**Hymenostylium recurvirostrum* (Hedw.) Dixon			
Waterton Lakes (townsite), Waterton Lakes Nat. Park	142	n = 13	40
	88	n = 13	41
Red Rock Canyon, Waterton Lakes Nat. Park	150	n = 13	42, 43
**Tortella tortuosa* (Turn.) Limpr.			
Mt. Burgess, Yoho Nat. Park	41	n = 13	44, 45
Bryoerythrophyllum recurvirostrum (Hedw.) Chen.			
L. Louise Station, Banff Nat. Park	48	n = 13	–
Baker Cr., Banff Nat. Park	99	n = 13	46, 47
Cameron Falls, Waterton Lakes Nat. Park	121	n = 13	–
Between Waterton Lakes and Alderson L., Waterton Lakes Nat. Park	149	n = 13	–
Pottia heimii (Hedw.) Fürnr.			
Beauty Cr., Jasper Nat. Park	23	n = 26	48
**Stegonia latifolia* (Schwaegr.) Vent			
Beauty Cr., Jasper Nat. Park	19	n = 26	49, 50
**Desmatodon latifolius* (Hedw.) Brid.			
Athabasca Glacier, Jasper Nat. Park	27	n = 26	51
Cameron L., Waterton Lakes Nat. Park.	116	n = 26	–
	120	n = 26	–
Carthew Lakes, Waterton Lakes Nat. Park	153	n = 26	52
Tortula mucronifolia Schwaegr.			
Kicking Horse Canyon, Yoho Nat. Park	54	n = 12	53
Johnson Canyon, Banff Nat. Park	131	n = 24	54, 55

Species and Source	Ref. No.	Chromosome No.	Illustrations
**Tortula ruralis* (Hedw.) Smith			
L. Louise, Banff Nat. Park	133	$n=12$	56, 57
GRIMMIACEAE			
**Grimmia affinis* Hornsch.			
Sunwapta Falls, Jasper Nat. Park	70	$n=13$	–
Kicking Horse Canyon, Yoho Nat. Park	80	$n=13$	58
**Grimmia alpicola* Hedw.			
Between Cameron L. and Carthew Lakes, Waterton Lakes Nat. Park	107	$n=13$	59
Carthew Lakes, Waterton Lakes Nat. Park	138	$n=13$	–
	139	$n=13$	60
	154	$n=13$	–
Grimmia alpicola var. *latifolia* (Zett.) C.M.			
Beauty Cr., Jasper Nat. Park	22	$n=13$	61, 62
Sunwapta Falls, Jasper Nat. Park	68	$n=13$	–
**Grimmia apocarpa* var. *pulvinata* (Hedw.) Jones			
Carthew Lakes, Waterton Lakes Nat. Park	136	$n=14$	63
**Grimmia montana* BSG			
Between Waterton Lakes and Bertha L., Waterton Lakes Nat. Park	113	$n=13$	64
FUNARIACEAE			
Funaria hygrometrica Hedw.			
Bow L., Banff Nat. Park	82	$n=14$	65
SPLACHNACEAE			
Splachnum ovatum Hedw.			
L. Louise Station, Banff Nat. Park	47	$n=9$	–
Between L. Louise and Moraine L., Banff Nat. Park	81	$n=9$	66
	89	$n=9$	–
L. O'Hara, Yoho Nat. Park	49	$n=9$	67
	50	$n=9$	–
	51	$n=9$	–
	52	$n=9$	–
BRYACEAE			
Pohlia cruda (Hedw.) Lindb.			
Sentinel Pass, above Moraine L., Banff Nat. Park	93	$n=40$	68, 69
Kicking Horse Canyon, Yoho Nat. Park	53	$n=10+4$	70, 71
**Leptobryum pyriforme* (Hedw.) Schimp.			
Banff, Banff Nat. Park	2	$n=20$	72
Sunwapta R., 9 mi. N. of Columbia Ice Field Chalet, Jasper Nat. Park	25	$n=20$	73

Species and Source	Ref. No.	Chromosome No.	Illustrations
Bryum pseudotriquetrum (Hedw.) Schwaegr.			
Baker Cr., Banff Nat. Park	30	n = 20	74
**Bryum pendulum* (Hornsch.) Schimp.			
Bow R. near Banff, Banff Nat. Park	100	n = 10	75
**Bryum turbinatum* (Hedw.) Schwaegr. (?)			
L. Louise Station, Banff Nat. Park	102	n = 10+1	76
MNIACEAE			
Mnium serratum Brid.			
Kiowa, Montana	141	n = 12	77
	14	n = 12	78
Near Jasper on Yellowhead Rd., Jasper Nat. Park	16	n = 12	–
Mnium spinulosum BSG			
Near Jasper on Yellowhead Rd., Jasper Nat. Park	17	n = 8	–
Bow L., Banff Nat. Park	58	n = 8	–
Cameron L., Waterton Lakes Nat. Park	118	n = 8	79
MEESIACEAE			
**Meesia uliginosa* Hedw.			
Baker Cr., Banff Nat. Park	31	n = 13	80, 81
CATOSCOPIACEAE			
**Catoscopium nigritum* (Hedw.) Brid.			
Edmonton Hwy., 16 mi. from Jasper, Jasper Nat. Park	62	n = 14	82, 83
BARTRAMIACEAE			
Bartramia ithyphylla Brid.			
L. Agnes, Banff Nat. Park	85	n = 12	84
Peyto L., Banff Nat. Park	105	n = 12	–
Philonotis fontana (Hedw.) Brid.			
Deep River, Ont.	76	n = 6	–
Between Cameron L. and Carthew Lakes, Waterton Lakes Nat. Park	106	n = 6	–
Cameron L., Waterton Lakes Nat. Park	147	n = 6	–
L. O'Hara, Yoho Nat. Park	55	n = 6	–
Bow L., Banff Nat. Park	134	n = 6	85, 86
TIMMIACEAE			
**Timmia austriaca* Hedw.			
Bow L., Banff Nat. Park	59	n = 16+1	87, 88

Species and Source	Ref. No.	Chromosome No.	Illustrations
ORTHOTRICHACEAE			
*_Orthotrichum alpestre_ Hornsch.			
Baker Cr., Banff Nat. Park	36	n=11	89
	40	n=11	–
	96	n=11	–
Bow L., Banff Nat. Park	60	n=11	–
	84	n=11	–
Continental Divide on Windermere Hwy., Banff Nat. Park	128	n=11	–
	9	n=11	–
	144	n=11	–
Orthotrichum rupestre Schleich.			
Sunwapta Falls, Jasper Nat. Park	71	n=6	90
*_Orthotrichum jamesianum_ Sull.			
Baker Cr., Banff Nat. Park	35	n=18	–
Banff, Banff Nat. Park	44	n=18	91
Bow L., Banff Nat. Park	61	n=18	–
	83	n=18	–
Carthew Lakes, Waterton Lakes Nat. Park	135	n=18	–
	137	n=18	–
Marble Canyon, Kootenay Nat. Park	146	n=18	92
Orthotrichum laevigatum Zett.			
Sunwapta Falls, Jasper Nat. Park	20	n=6	–
	66	n=6	–
L. Louise, Banff Nat. Park	72	n=6	93
	65	n=6	–
Continental Divide on Windermere Hwy., Banff Nat. Park	12	n=6	–
*_Orthotrichum roellii_ Vent.			
Baker Cr., Banff Nat. Park	34	n=6	94, 95
*_Orthotrichum sordidum_ Sull. & Lesq.			
Scott Falls, Au Train, Mich	1	n=6	96
	132	n=6	97
Near Munising, Mich	29	n=6	–
Orthotrichum speciosum Nees			
Banff, Banff Nat. Park	45	n=6	–
	56	n=6	–
L. Louise, Banff Nat. Park	64	n=6	–
Baker Cr., Banff Nat. Park	95	n=6	98
Orthotrichum texanum Sull.			
Near Jasper on Yellowhead Rd., Jasper Nat. Park	46	n=6	99
Ulota cirrata (Bernh.) Grout			
L. O'Hara, Yoho Nat. Park	57	n=20+2	–
	78	n=20+2	100, 101
AMBLYSTEGIACEAE			
Cratoneuron falcatum (Brid.) Roth			
Baker Cr., Banff Nat. Park	33	n=7	102, 103

Species and Source	Ref. No.	Chromosome No.	Illustrations
Amblystegium juratzkanum Schimp.			
Near Munising, Mich.	37 *p.p.*	$n=12+1$	104
**Amblystegium varium* (Hedw.) Lindb.			
Near Munising, Mich.	37 *p.p.*	$n=12+1$	105, 106
Campylium stellatum (Hedw.) Lange & C. Jens.			
Between L. Louise and Moraine L., Banff Nat. Park	140	$n=18+2$	107, 108
Drepanocladus uncinatus (Hedw.) Warnst.			
Near Jasper on Yellowhead Rd., Jasper Nat. Park	3	$n=20$	109, 110
Maligne Canyon, Jasper Nat. Park	13	$n=20$	–
Baker Cr., Banff Nat. Park	103	$n=20$	–
L. Louise, Banff Nat. Park	5	$n=20$	–
Cameron L., Waterton Lakes Nat. Park.	90	$n=12$	111
**Hygrohypnum luridum* fo. *julaceum* (BSG) C. Jens.			
Baker Cr., Banff Nat. Park	39	$n=10+1$	–
Kimpton Cr., below Sinclair Pass, Kootenay Nat. Park	86	$n=10+1$	112, 113
PLAGIOTHECIACEAE			
Plagiothecium denticulatum (Hedw.) BSG			
Bow L., Banff Nat. Park	79	$n=25$	114–116
HYPNACEAE			
Hypnum cupressiforme Hedw.			
Banff, Banff Nat Park	6	$n=16$	117–119
**Hypnum revolutum* (Mitt.) Lindb.			
L. Louise Station, Banff Nat. Park	101	$n=14$	120, 121
**Isopterygium pulchellum* (Hedw.) Jaeg.			
Between Waterton Lakes and Bertha L.	115	$n=11$	122–124
Baker Cr., Banff Nat. Park	32	$n=22$	125
Ptilium crista-castrensis (Hedw.) DeNot.			
Mt. Robson Station, Mt. Robson Provincial Park	77	$2n=20$ $n=10+1$	126, 127 128, 129
POLYTRICHACEAE			
Pogonatum alpinum (Hedw.) Röhl.			
Between Waterton Lakes and Bertha L., Waterton Lakes Nat. Park	110	$n=7$	130
Pogonatum alpinum var. *septentrionale* (Röhl.) Brid.			
Sentinel Pass, above Moraine L., Banff Nat. Park	92	$n=7$	131

Species and Source	Ref. No.	Chromosome No.	Illustrations
Polytrichum juniperinum Hedw.			
L. Louise, Banff Nat. Park............	73	n = 7	–
Baker Cr., Banff Nat. Park............	97	n = 7	132
Polytrichum piliferum Hedw.			
Between Cameron Cr. and Upper Rowe Lakes, Waterton Lakes Nat. Park....	151	n = 7	133
**Polytrichadelphus lyallii* Mitt.			
Between Waterton Lakes and Bertha L., Waterton Lakes Nat. Park..........	109	n = 7	134, 135
Alderson L., Waterton Lakes Nat. Park............................	123	n = 7	–

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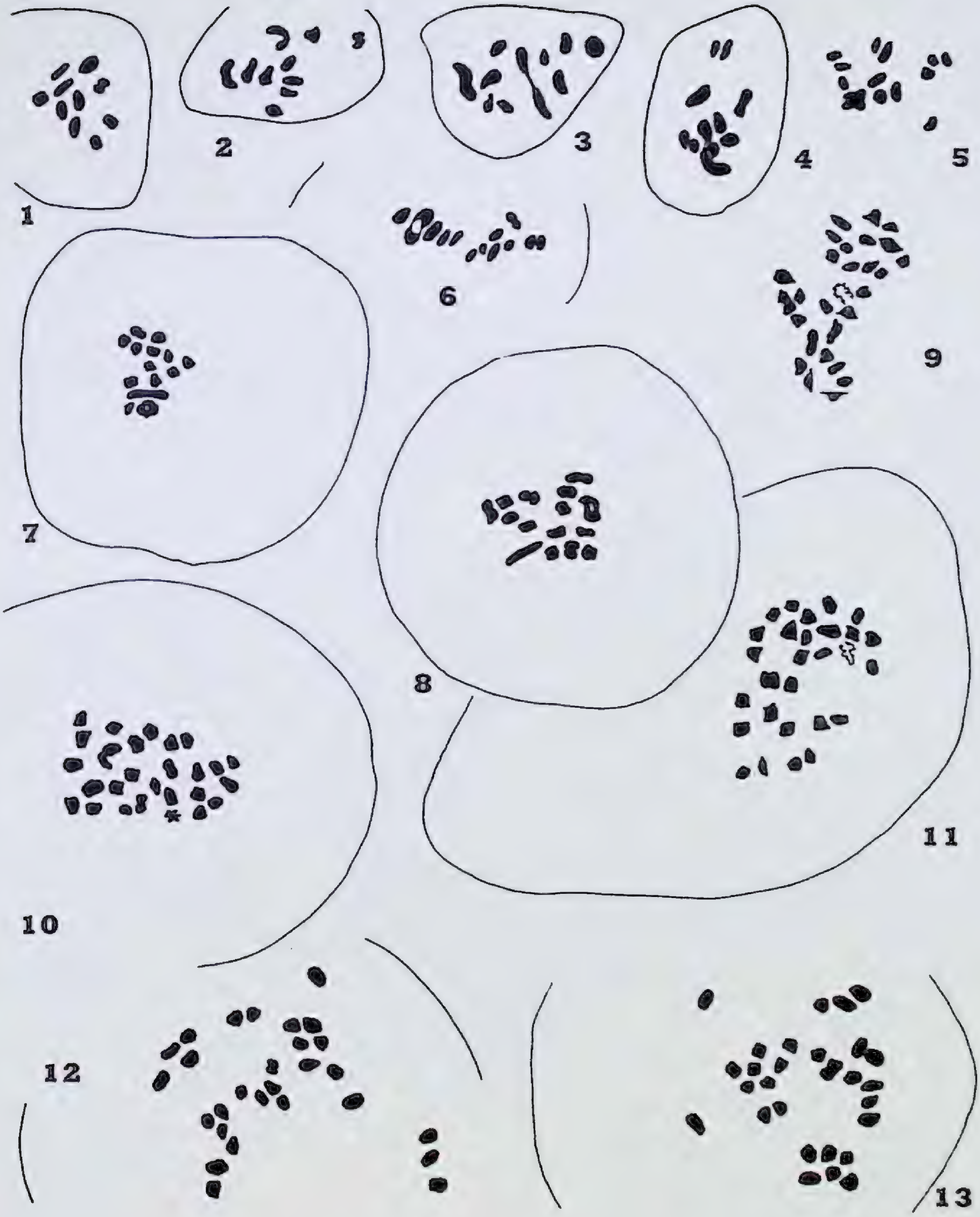
Figures 1–4. *Fissidens bryoides* Hedw., n=10; figs. 1–2, early MI in polar view; note size differences among bivalents; figs. 3, 4, late MI, side view with chromosomes spread apart; bivalents are beginning to disjoin.

Figures 5–6. *Ceratodon purpureus* (Hedw.) Brid., n=13; fig. 5, early MI in polar view, showing the large bivalent prior to opening out; fig. 6, later MI, showing separation of the large bivalent in advance of the other bivalents.

Figures 7–13. *Distichium capillaceum* (Hedw.) BSG, n=14, n=28; fig. 7, MI, showing 14 bivalents, including one O-type bivalent; fig. 8, later stage of MI, showing 13 bivalents and two half-bivalents which have separated precociously (lower right centre); figs. 9–11, polar view of MI figures of tetraploid population from Bow River near Banff, showing 28 bivalents, including one bivalent which has failed to condense; note large size of SMC as compared with the diploid population; figs. 12, 13, polar view of MI from tetraploid population from Sunwapta River, showing 28 bivalents; note that in this population all bivalents are condensed.



Figures 14, 15. *Dicranella crispa* (Hedw.) Schimp., n=14; polar views of early or prometaphase figures; note the characteristic configuration of the large bivalent in both figures.

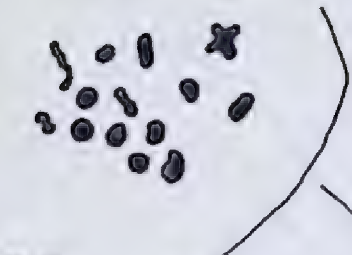
Figures 16–21. *Dicranella subulata* (Hedw.) Schimp., n=14+1; fig. 16, early MI, showing small m-bivalent separating early; fig. 17, MI, in which m-bivalent has separated into four small, lightly-staining chromatids; figs. 18–20, three MI figures, each showing 14 bivalents, the m-bivalent having dissociated into a half-bivalent and two chromatids (arrows); fig. 21, flattened AI, in which the four chromatids of the m-bivalent are visible (arrows).

Figure 22. *Amphidium lapponicum* Schimp., n=16; side view of MI, showing 16 bivalents.

Figures 23–25. *Cynodontium strumiferum* (Hedw.) DeNot., n=14; figs. 23, 24, side views of MI, showing stages in the premature separation of the small bivalent; figure 25, polar view of MI, showing 13 large bivalents and one small bivalent.

Figures 26, 27. *Dicranoweisia crispula* (Hedw.) Lindb., n=11; fig. 26, early MI, showing two bivalents beginning to disjoin early; fig. 27, later MI, showing sticky connections between separating half-bivalents.

Figure 28. *Oncophorus virens* (Hedw.) Brid., n=14; early MI or late diakinesis showing 14 bivalents; one is disjoining prematurely. The bizarre shapes of bivalents are caused by excess pressure on the cover glass during preparation procedures.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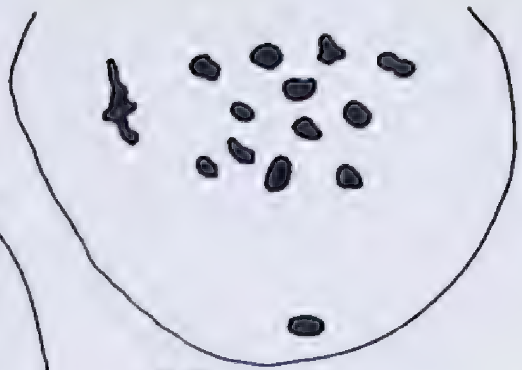
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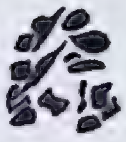
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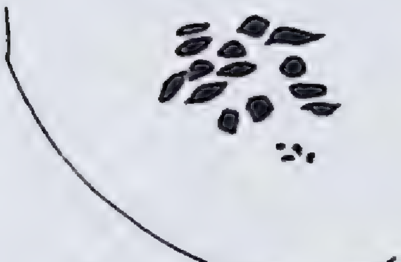
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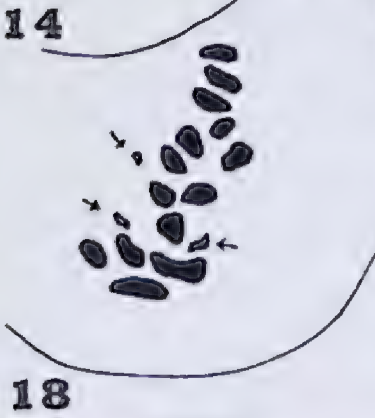
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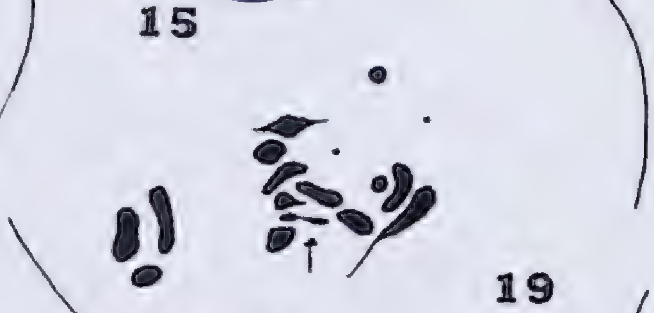
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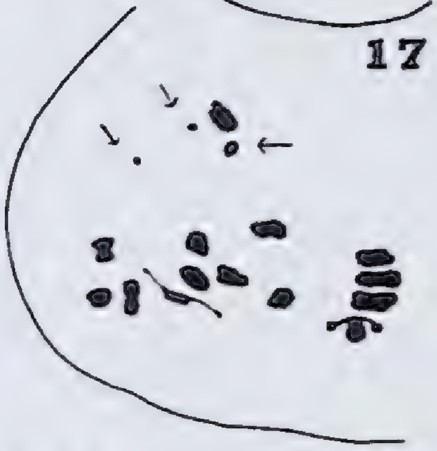
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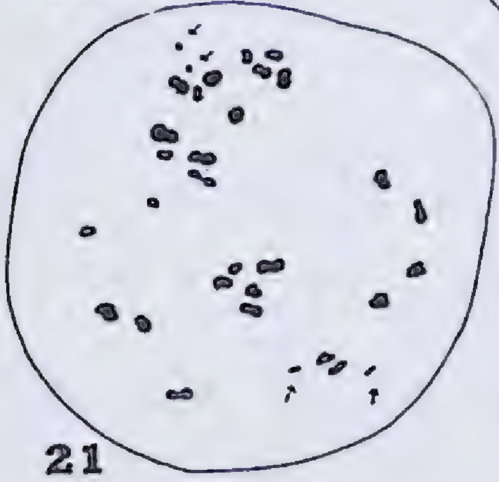
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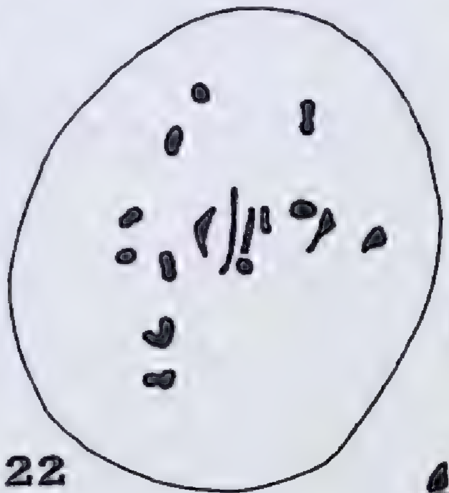
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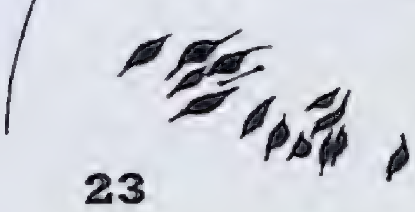
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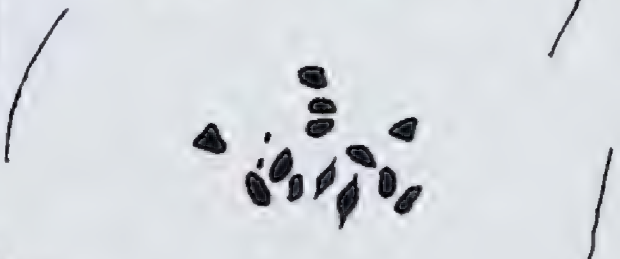
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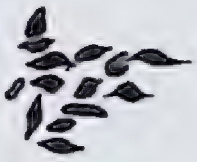
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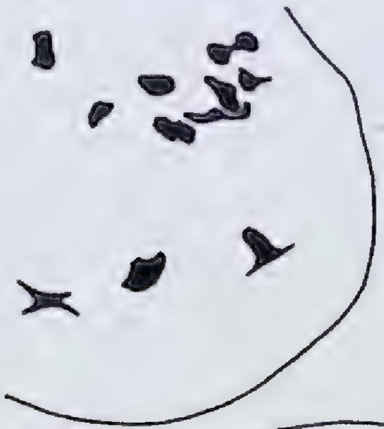
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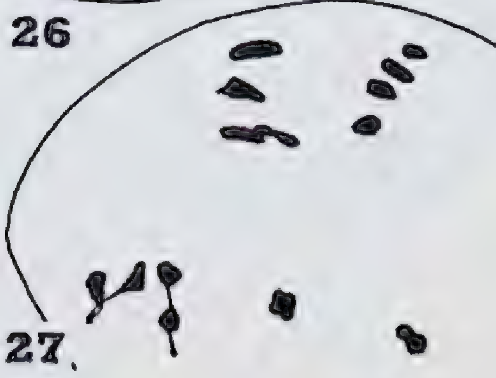
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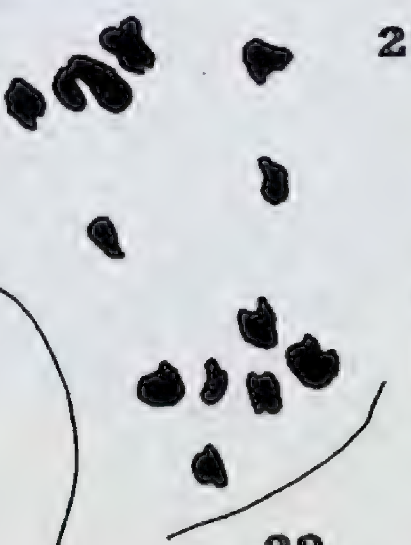
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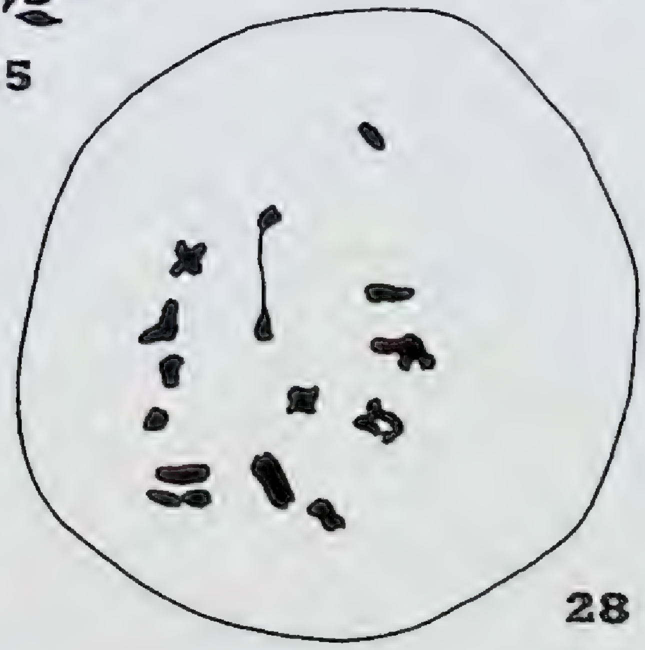
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Figures 29-34. *Dicranum fuscescens* Turn., n=12, n=24; figs. 29, 30, late diakinesis figures showing 12 bivalents in each; note one large bivalent in each figure which appears to contain a heterochromosome; figs. 31, 32, MI figures from a tetraploid population in which 24 bivalents are present; fig. 33, AI, showing lagging chromosome fragment which fails to move on the spindle and is eliminated from the complement; fig. 34, polar view of MI from diploid population showing a small chromosome fragment which is eliminated during AI.

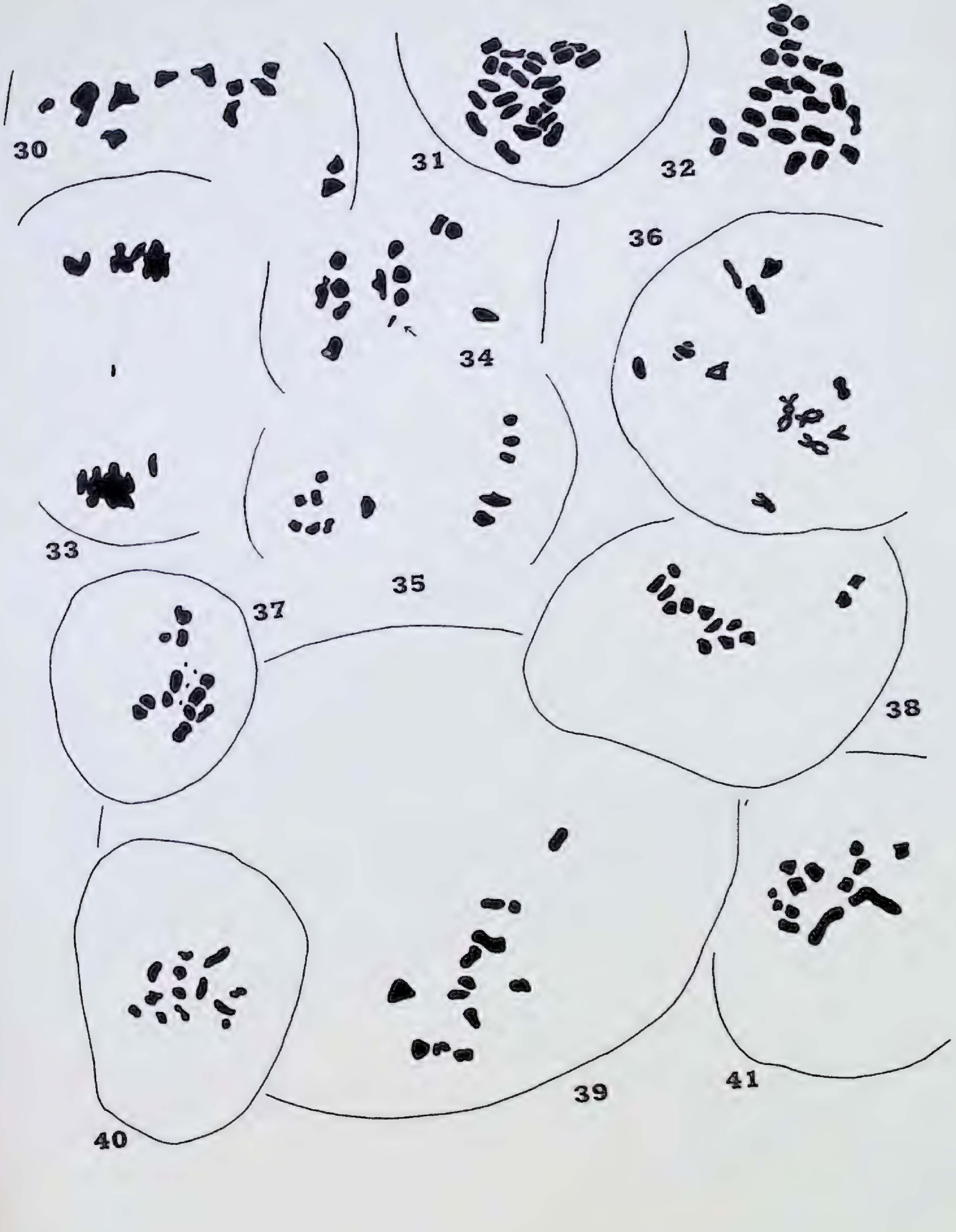
Figures 35, 36. *Dicranum groenlandicum* Brid., n=12; fig. 35, polar view of MI, showing 12 bivalents; fig. 36, late diakinesis.

Figure 37. *Dicranum strictum* Schleich., n=12+2; polar view of MI, showing 12 large bivalents plus four half-bivalents which have resulted from premature disjunction of two small bivalents.

Figure 38. *Encalypta apophysata* Nees & Hornsch., n=13; side view of early MI, showing 13 bivalents.

Figure 39. *Encalypta ciliata* Hedw., n=13; polar view of MI, showing 13 bivalents; note large size of SMC as compared with that in fig. 38.

Figures 40–43. *Hymenostylium recurvirostrum* (Hedw.) Dixon, n=13; fig. 40, polar view of MI; fig. 41, polar view of late MI; note stretching of separating half-bivalents; fig. 42, late diakinesis; fig. 43, polar view of MI; note size variation in chromosomes.



Figures 44, 45. *Tortella tortuosa* (Turn.) Limpr., n=13; fig. 44, side view of MI, showing three bivalents disjoining; fig. 45, polar view of early MI; note small size of SMC as well as small chromosomes.

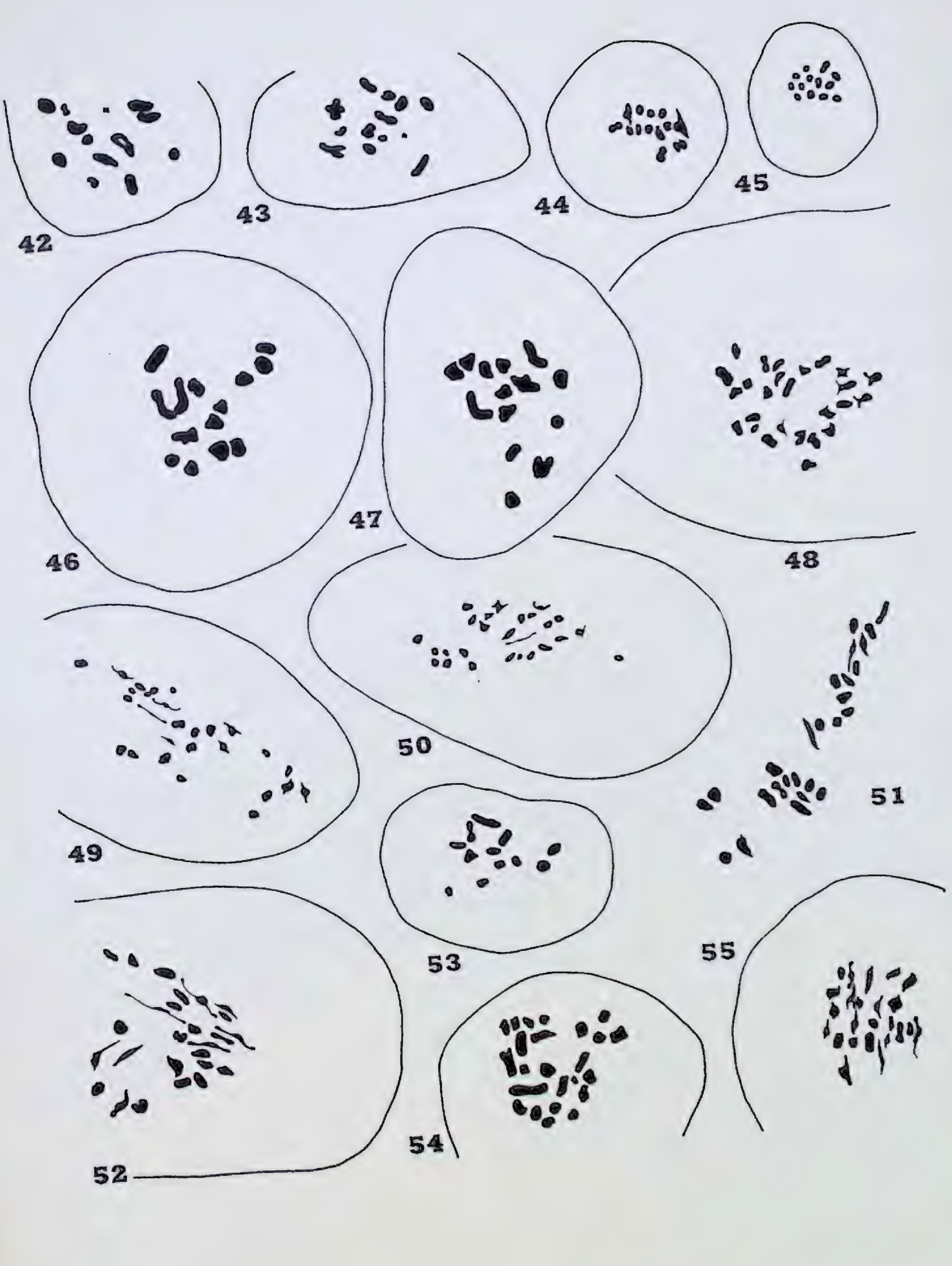
Figures 46, 47. *Bryoerythrophyllum recurvirostrum* (Hedw.) Chen., n=13; fig. 46, polar view of early MI, showing 13 bivalents, including one large bivalent about to disjoin; fig. 47, later stage, showing two large half-bivalents having already disjoined, and 12 bivalents.

Figure 48. *Pottia heimii* (Hedw.) Fürnr., n=26; polar view of MI, showing 26 bivalents.

Figures 49, 50. *Stegonia latifolia* (Schwaegr.) Vent., n=26; polar views of MI, showing characteristically attenuated bivalents.

Figures 51, 52. *Desmatodon latifolius* (Hedw.) Brid., n=26; fig. 51, side view of MI, showing 26 bivalents; fig. 52, polar view of MI, showing effects of extreme pressure of flattening on chromosomes.

Figures 53–55. *Tortula mucronifolia* Schwaegr., n=12, n=24; fig. 53, polar view of MI from diploid population (No. 54), showing 12 bivalents; figs. 54, 55, polar and side views, respectively, of tetraploid population (No. 131), showing in each 24 bivalents.



Figures 56, 57. *Tortula ruralis* (Hedw.) Smith, n=12; fig. 56, side view of MI, showing 12 bivalents; fig. 57, polar view of MI, showing one bivalent beginning to disjoin.

Figure 58. *Grimmia affinis* Hornsch., n=13; side view of MI, showing 13 bivalents becoming aligned on the plate.

Figures 59, 60. *Grimmia alpicola* Hedw., n=13; fig. 59, side view of early AI; seven bivalents (still at metaphase I) are undissociated; the other bivalents are in early anaphase, with two disjoining and four already disjoined; fig. 60, side view of MI, with 12 intact bivalents and two half-bivalents.

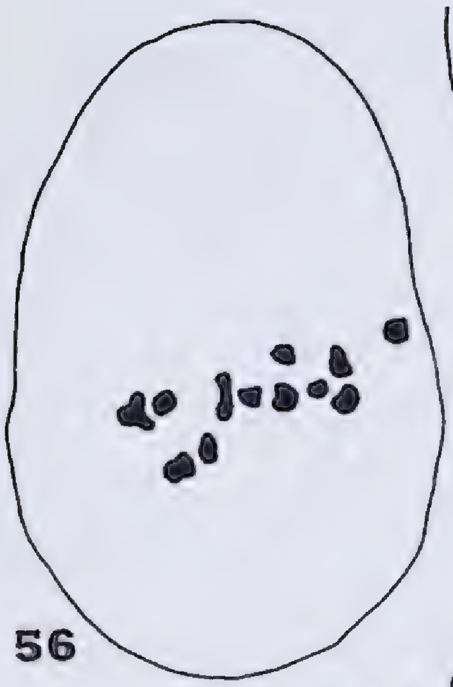
Figures 61, 62. *Grimmia alpicola* var. *latifolia* (Zett.) C.M., n=13; polar views of MI, showing in each figure, 13 bivalents.

Figure 63. *Grimmia apocarpa* var. *pulvinata* (Hedw.) Jones, n=14; polar view of MI, showing 14 bivalents.

Figure 64. *Grimmia montana* BSG, n=13; side view of MI, showing 12 bivalents and two half-bivalents which have separated prematurely.

Figure 65. *Funaria hygrometrica* Hedw., n=14; polar view of MI, showing 14 bivalents.

Figures 66, 67. *Splachnum ovatum* Hedw., n=9; polar views of MI, both with a haploid number of nine; the two drawings are from different populations; note similarity between complements.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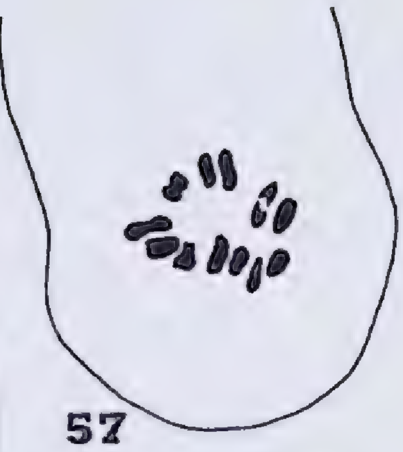
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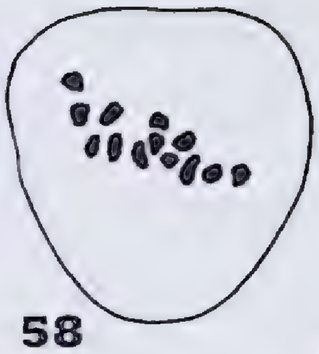
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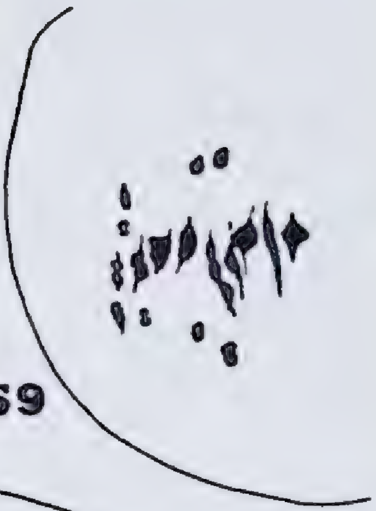
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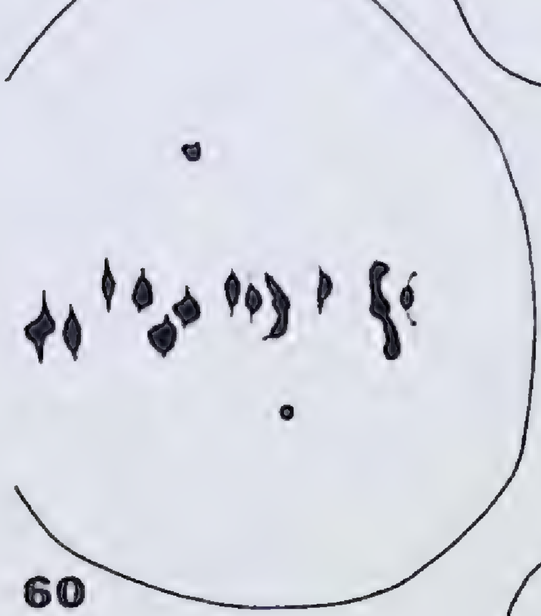
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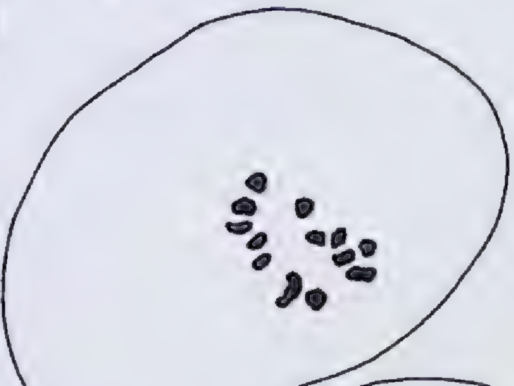
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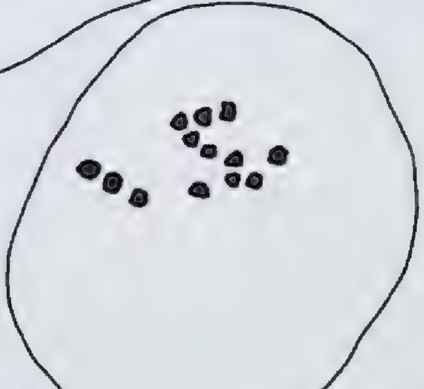
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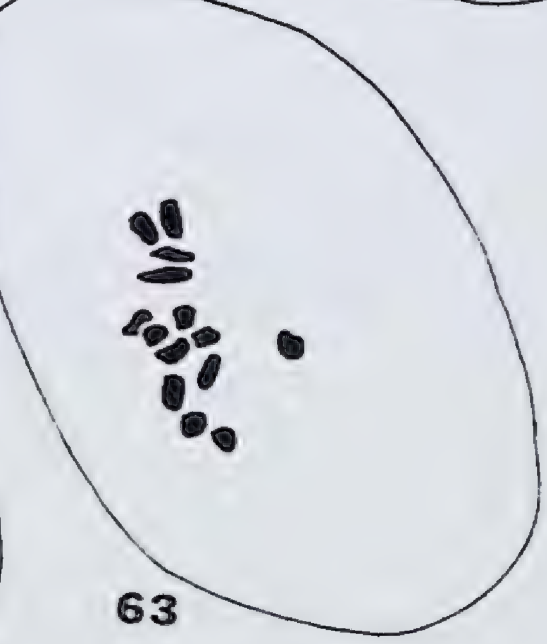
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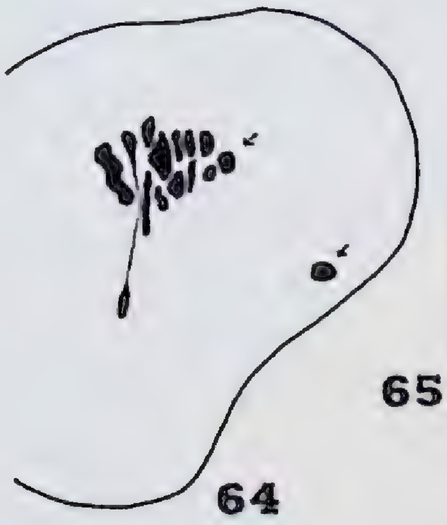
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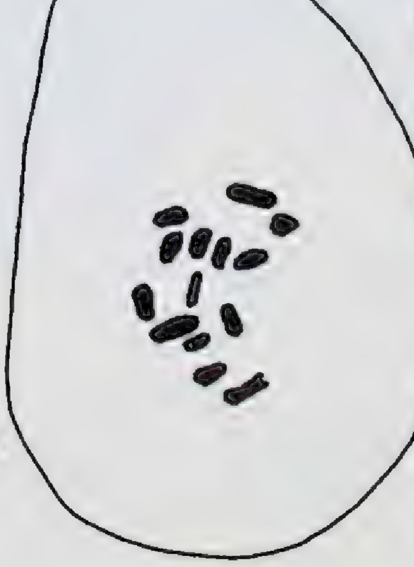
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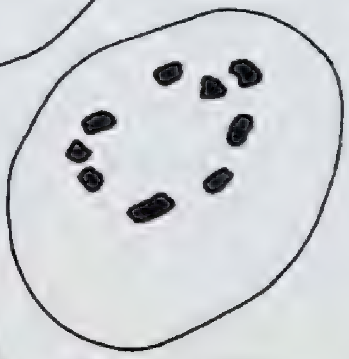
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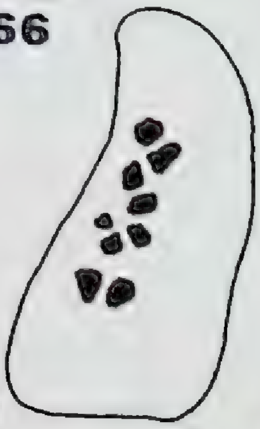
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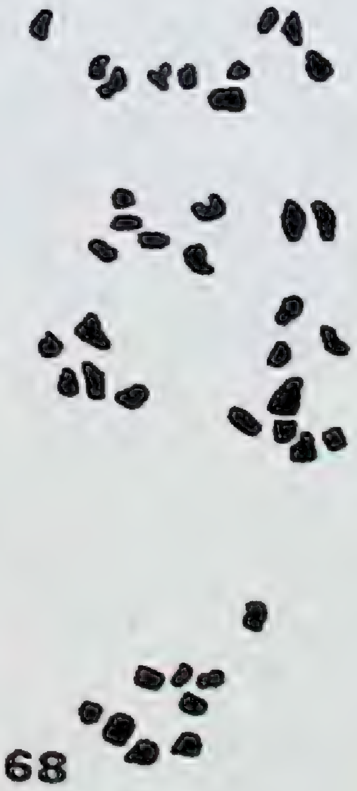
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Figures 68–71. *Pohlia cruda* (Hedw.) Lindb., n=10+4, n=40; fig. 68, metaphase chromosomes drawn from ruptured cell whose cytoplasm had partially escaped from the cell wall; a total of 40 bivalents are discernible; fig. 69, polar view of MI, showing 40 bivalents; note large size of SMC as compared with 10-chromosome population; fig. 70, polar view of MI, showing 10 large bivalents, plus four m-bivalents, each of which has separated prematurely into two half-bivalents; fig. 71, polar view of MI, in which two m-bivalents have each separated into their respective four chromatids, while the other two m-bivalents have disjoined, forming two half-bivalents.

Figures 72, 73. *Leptobryum pyriforme* (Hedw.) Schimp., n=20; polar view of MI with 20 bivalents; note single large bivalent characteristic also of the genus *Bryum*.

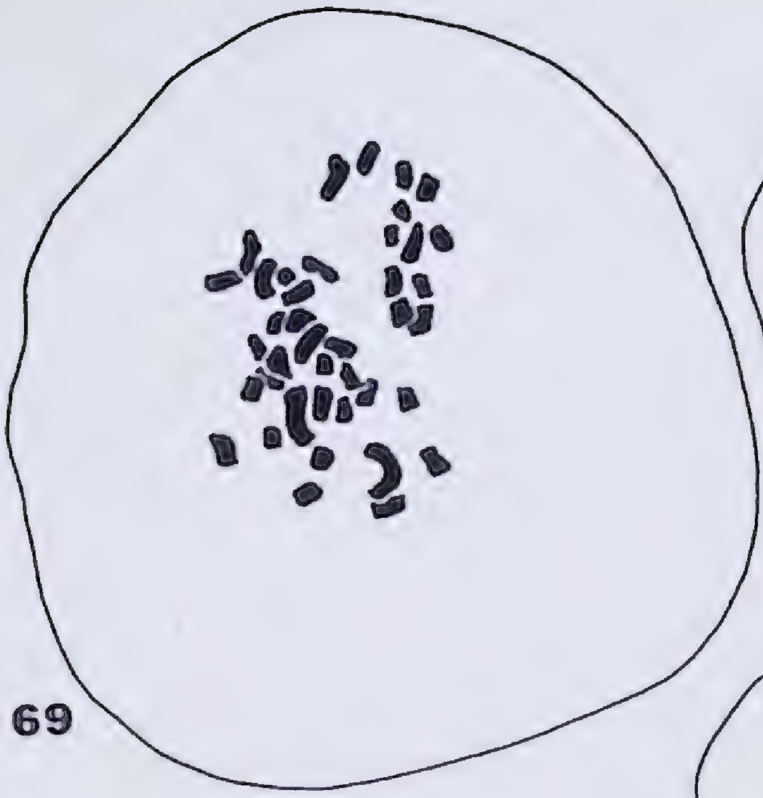
Figure 74. *Bryum pseudotriquetrum* (Hedw.) Schwaegr., n=20; side view of MI; 20 bivalents are distinguishable.

Figure 75. *Bryum pendulum* (Hornsch.) Schimp., n=10; polar view of early MI, showing 10 bivalents.

Figure 76. *Bryum turbinatum* (Hedw.) Schwaegr. (?), n=10+1; polar view of early MI, showing 10 large bivalents, one of which is disjoining prematurely, and two tiny half-bivalents which originated from a small m-like chromosome.

Figures 77, 78. *Mnium serratum* Brid., n=12; fig. 77, side view of early MI, showing 12 bivalents, including an O-type bivalent; fig. 78, SMC with A2 chromosomes pressed out into one plane, with 48 chromosomes visible; the four original anaphasic groupings can be more or less distinguished.

Figure 79. *Mnium spinulosum* BSG, n=8; side view of late AI, showing eight half-bivalents moving toward each pole; note the somatic-like nature of the anaphasic chromosomes.



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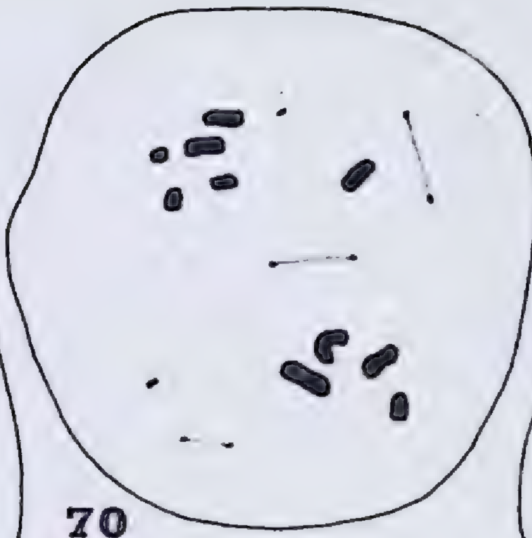

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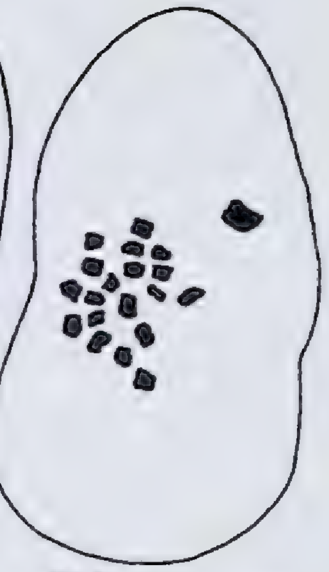

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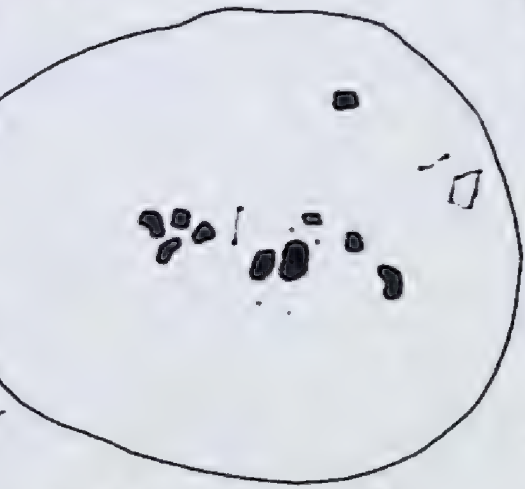

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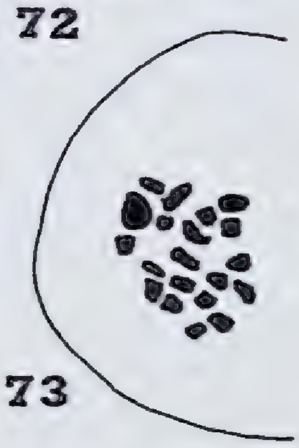

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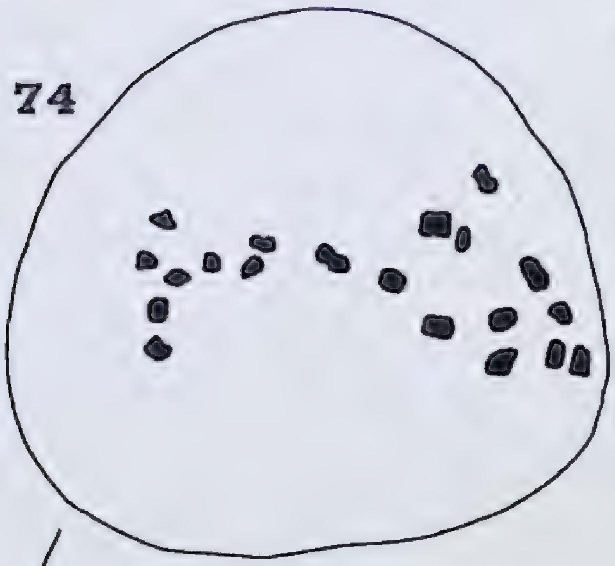

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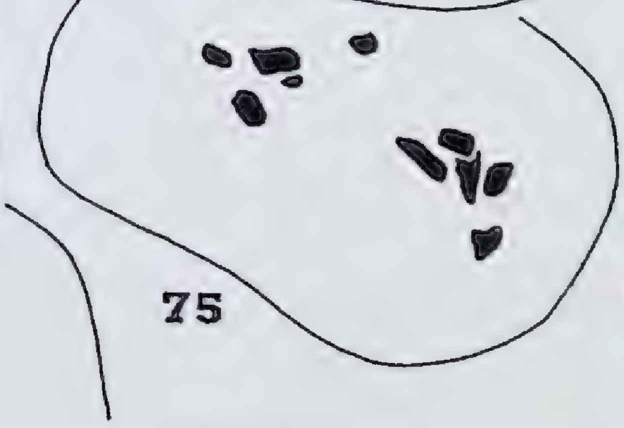

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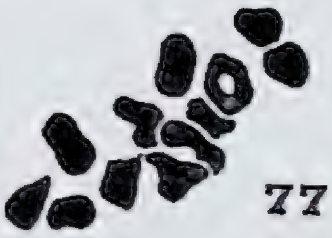

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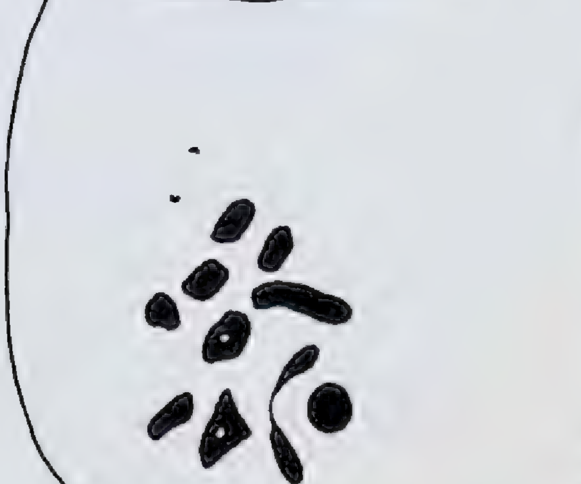

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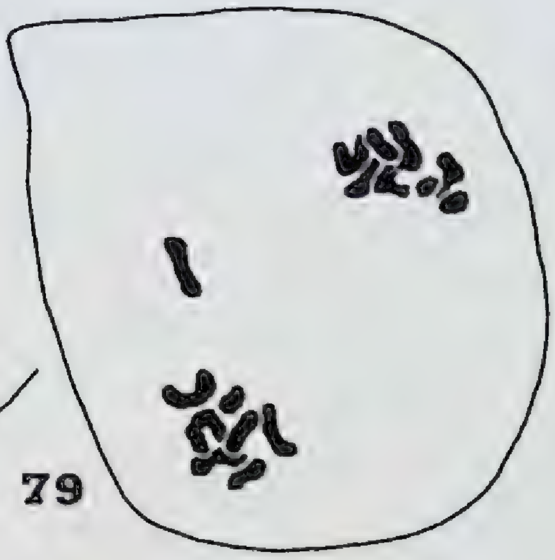

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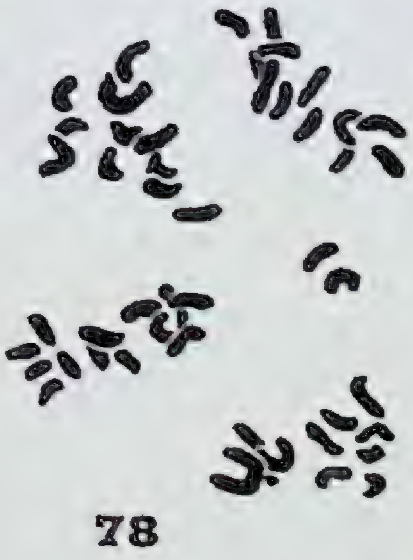

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Figures 80, 81. *Meesia uliginosa* Hedw., n=13; fig. 80, AI, with 13 half-bivalents visible near each pole; note two smaller half-bivalents which are lagging; fig. 81, side view of MI, showing 13 bivalents.

Figures 82, 83. *Catoscopium nigritum* (Hedw.) Brid., n=14; fig. 82, side view of MI, showing separating bivalents; two bivalents have already disjoined; fig. 83, polar view of MI, showing 14 bivalents, one of which is disjoining.

Figure 84. *Bartramia ithyphylla* Brid., n=12; polar view of MI, showing 12 large and uniformly-sized bivalents. Bivalents stain faintly with acetic orcein.

Figures 85, 86. *Philonotis fontana* (Hedw.) Brid., n=6; fig. 85, side view of MI, showing five bivalents and two half-bivalents; fig. 86, polar view of MI, showing six bivalents.

Figures 87, 88. *Timmia austriaca* Hedw., n=16+1; fig. 87, polar view of MI, showing 16 large bivalents plus one small bivalent; fig. 88, polar view of MI, showing precocious division of the small bivalent; the 16 larger bivalents are undivided.

Figure 89. *Orthotrichum alpestre* Hornsch., n=11, side view of MI, showing 10 large bivalents with one bivalent having disjoined early to form two half-bivalents.

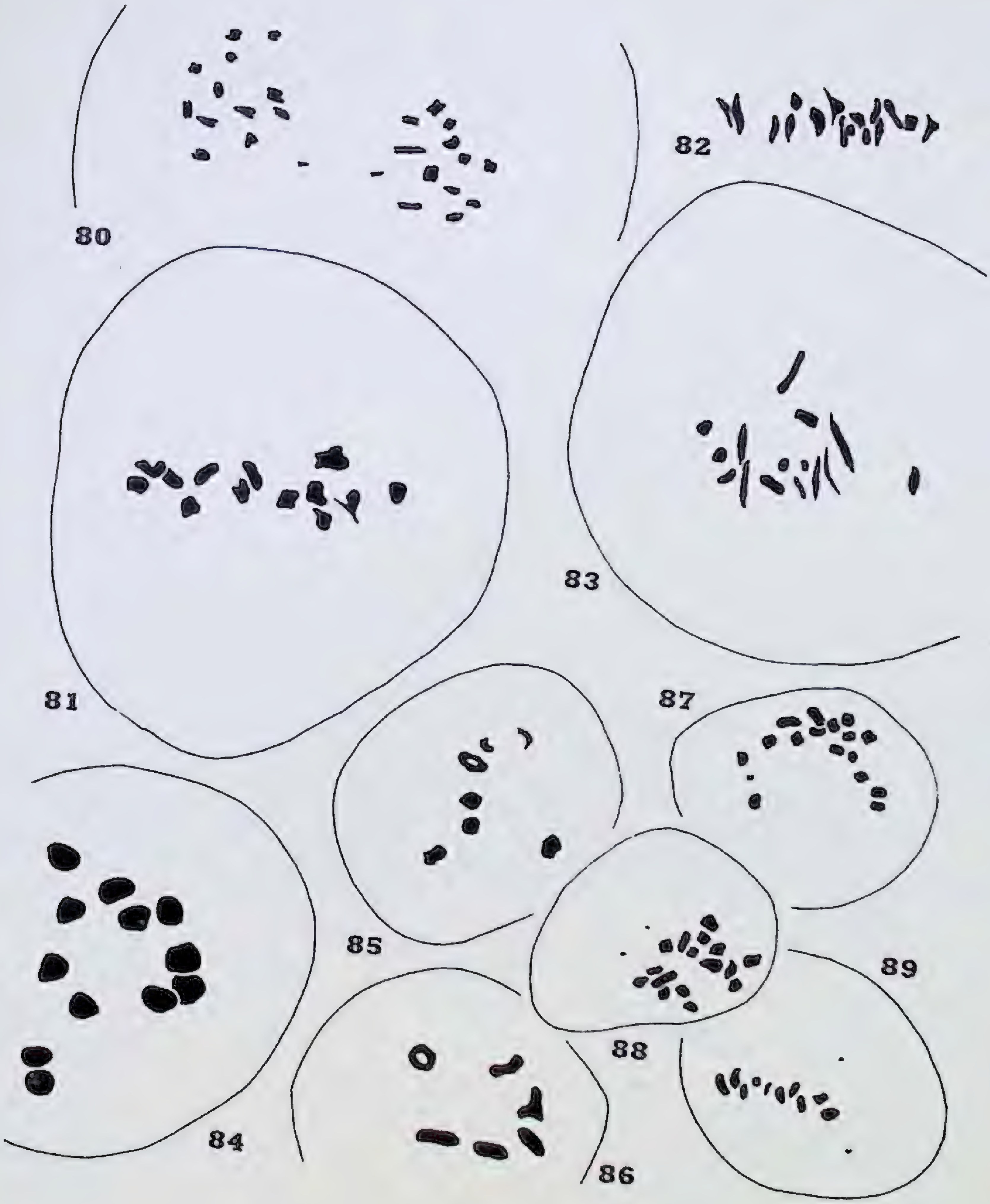


Figure 90. *Orthotrichum rupestre* Schleich., n=6; polar view of early MI, showing six bivalents. Note the one large, long bivalent characteristic of 6-chromosome species.

Figures 91, 92. *Orthotrichum jamesianum* Sull., n=18; fig. 91, polar view of MI, showing 18 bivalents; fig. 92, later stage showing two bivalents, one large and one small, disjoining.

Figure 93. *Orthotrichum laevigatum* Zett., n=6; polar view of MI plate, showing 6 bivalents; the smallest bivalent in the near centre of the group divides prematurely.

Figures 94, 95. *Orthotrichum roellii* Vent., n=6; fig. 94, polar view of MI plate, showing six bivalents, the smallest of which is disjoining; fig. 95, late AII, showing six chromosomes in each of the four anaphasic groups; note that in one group the sister chromatids of one chromosome are distinguishable.

Figures 96, 97. *Orthotrichum sordidum* Sull. & Lesq., n=6; fig. 96, late diakinesis, showing six bivalents; fig. 97, side view of MI; the small bivalent has already disjoined while the five large bivalents are just beginning to separate.

Figure 98. *Orthotrichum speciosum* Nees, n=6; side view of late AI, showing two half-bivalents which are late in disjoining.

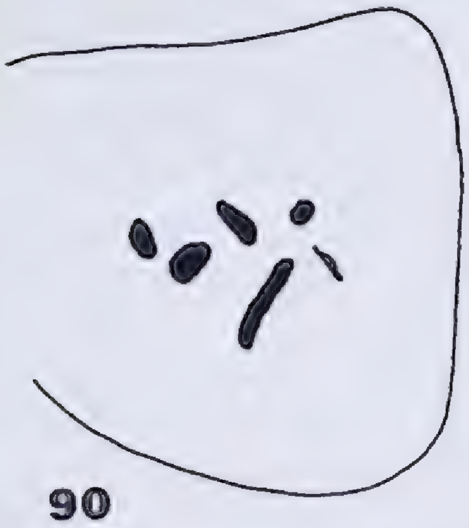
Figure 99. *Orthotrichum texanum* Sull., n=6; polar view of MI, showing six bivalents.

Figures 100, 101. *Ulota cirrata* (Bernh.) Grout, n=20+2; fig. 100, polar view of MI, showing 20 large bivalents, with two smaller bivalents having previously disjoined; fig. 101, earlier stage with 20 large bivalents, one small bivalent and two small half-bivalents.

Figures 102, 103. *Cratoneuron falcatum* (Brid.) Roth, n=7; polar views of MI, each with seven bivalents; note small SMC and small compact chromosomes.

Figure 104. *Amblystegium juratzkanum* Schimp., n=12+1; polar view of MI, showing 12 large bivalents and one small bivalent; note that one of the larger bivalents has begun to disjoin.

Figures 105, 106. *Amblystegium varium* (Hedw.) Lindb., n=12+1; polar view of MI figures showing in each 12 large bivalents and one small bivalent which has already disjoined.



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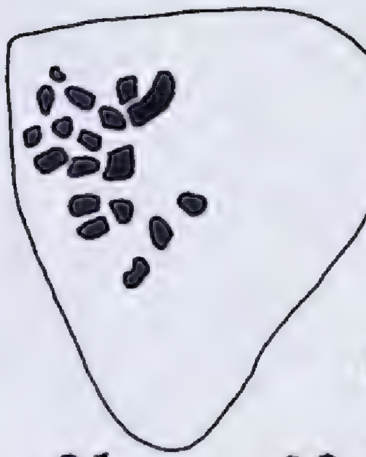

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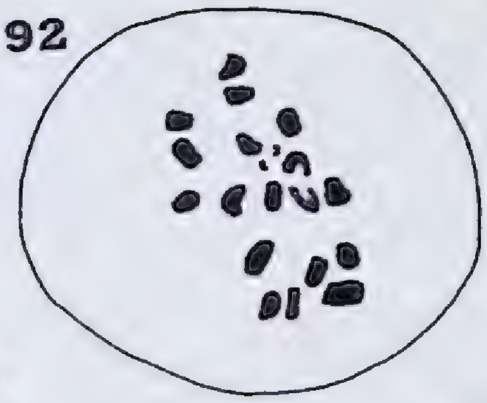

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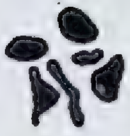

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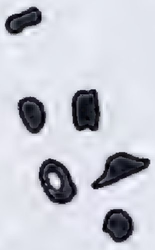

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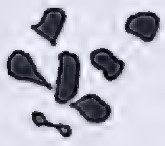

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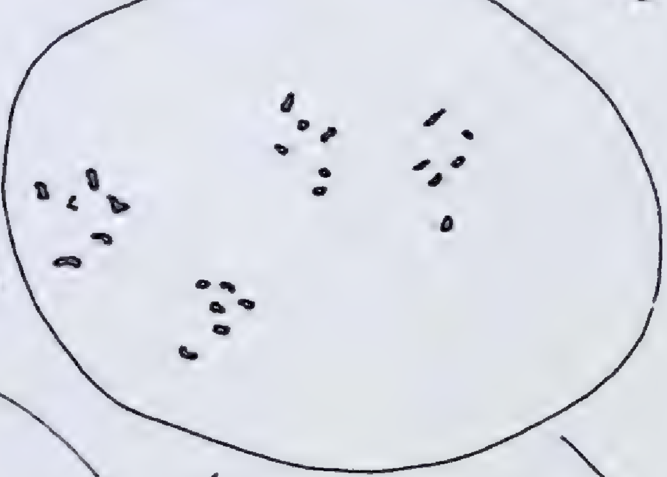

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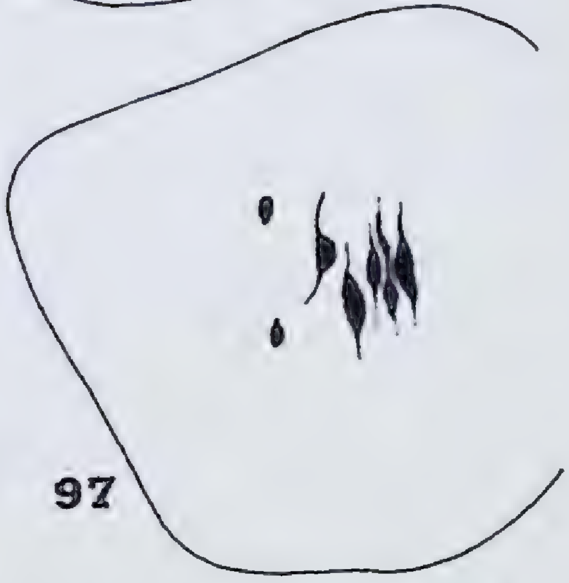

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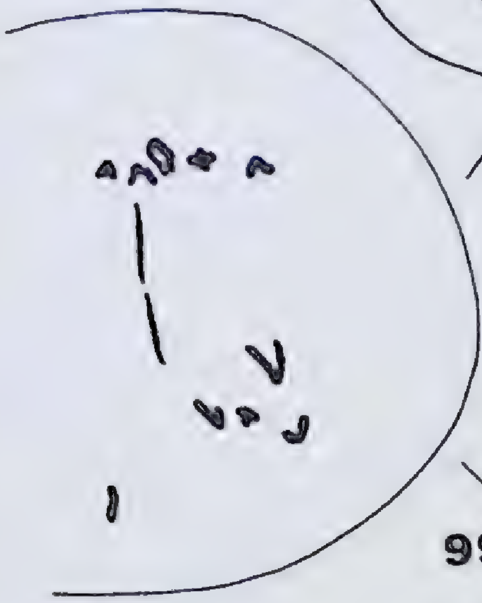

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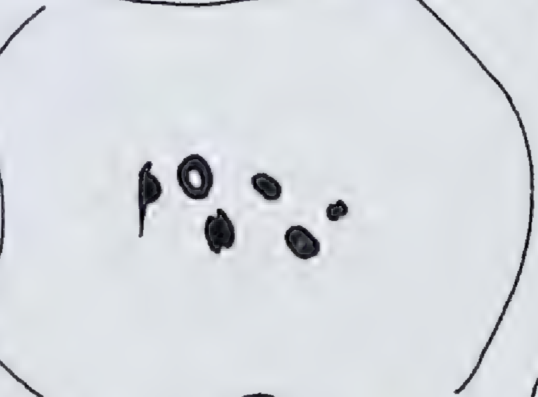

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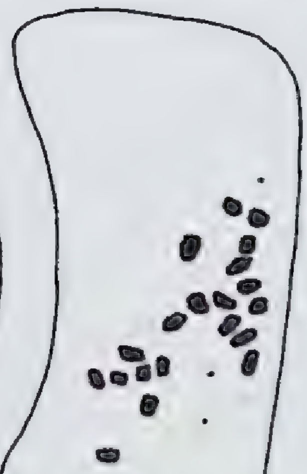

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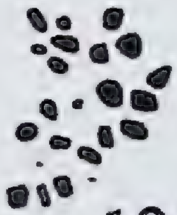

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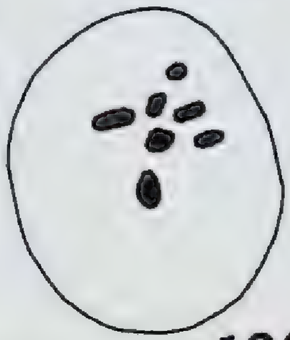

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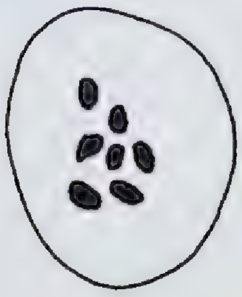

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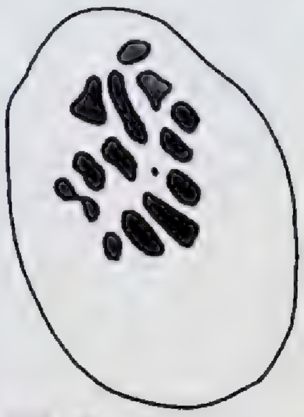

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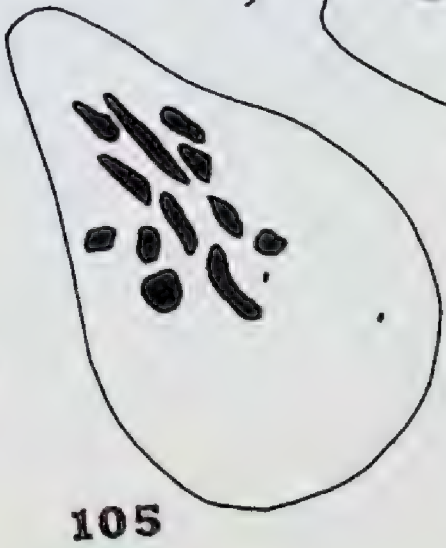

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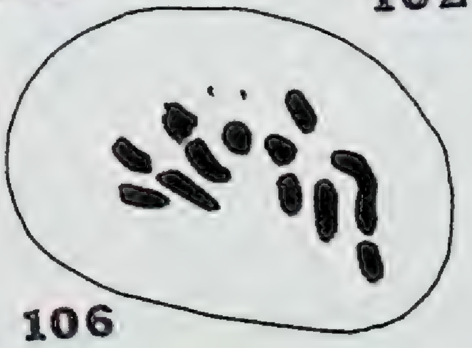

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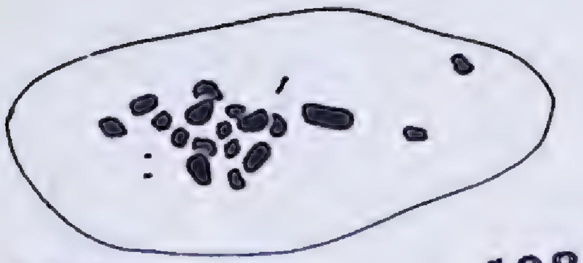
Figures 107, 108. *Campylium stellatum* (Hedw.) Lange & C. Jens., n=18+2; fig. 107, polar view of MI, showing 18 large bivalents and two prematurely dissociating bivalents, one of which has completely disjoined; fig. 108, later stage in which one of the small bivalents has broken up into its respective four chromatids.

Figures 109–111. *Drepanocladus uncinatus* (Hedw.) Warnst., n=12, n=20; fig. 109, prometaphase, in which four groups of four bivalents each are associated together; four additional bivalents make a total of 20 bivalents; fig. 110, polar view of MI, showing 20 bivalents; the associated bivalents seen in the previous figure are now separated; fig. 111, SMC from a population in which there are only 12 bivalents; polar view of MI.

Figures 112, 113. *Hygrohypnum luridum* fo. *julaceum* (BSG) C. Jens., n=10+1; fig. 112, polar view of MI, with 10 large and one small bivalent; fig. 113, same, showing precocious separation of the small bivalent.

Figures 114–116. *Plagiothecium denticulatum* (Hedw.) BSG, n=25; polar views of MI figures showing in each 25 bivalents. Note the large bivalent which is recognizable in each mother cell.

Figures 117–119. *Hypnum cupressiforme* Hedw., n=16; polar views of MI, showing 16 bivalents.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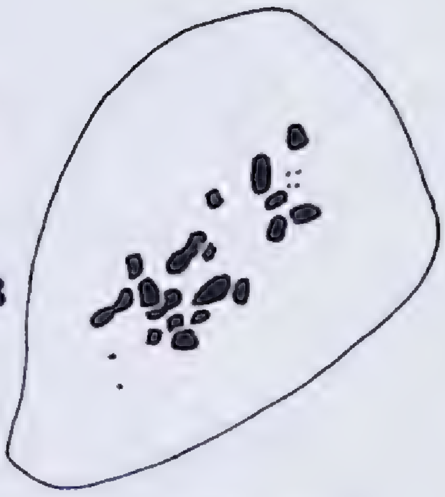
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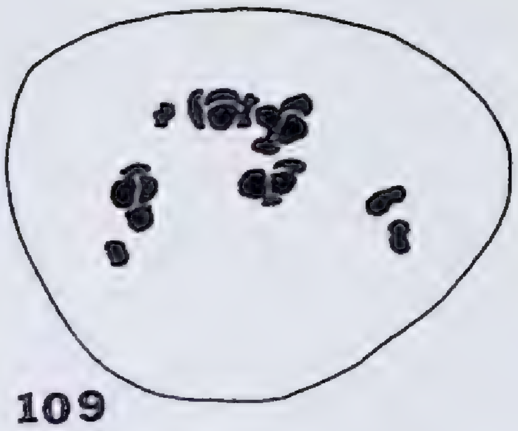
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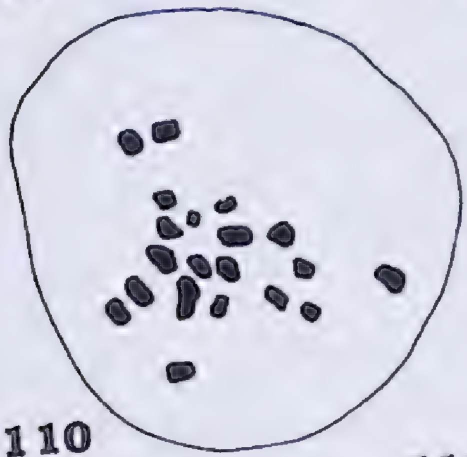
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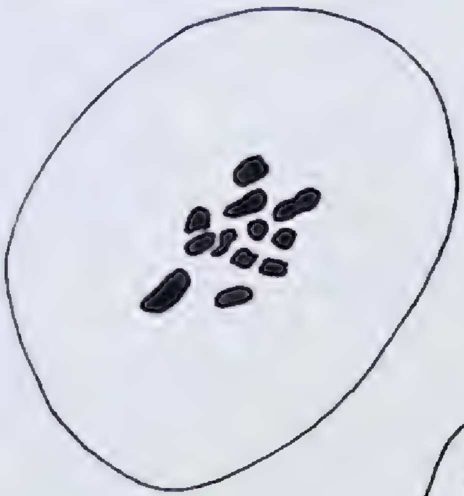
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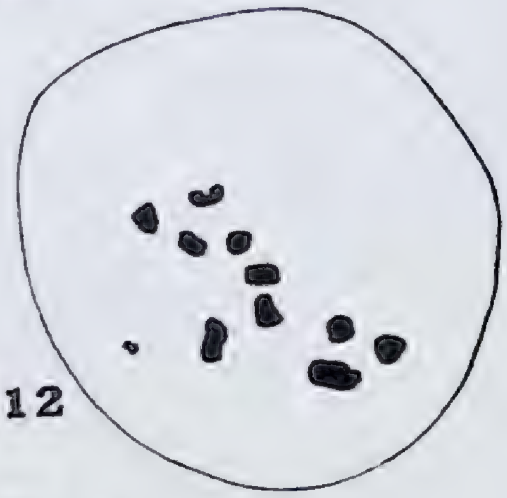
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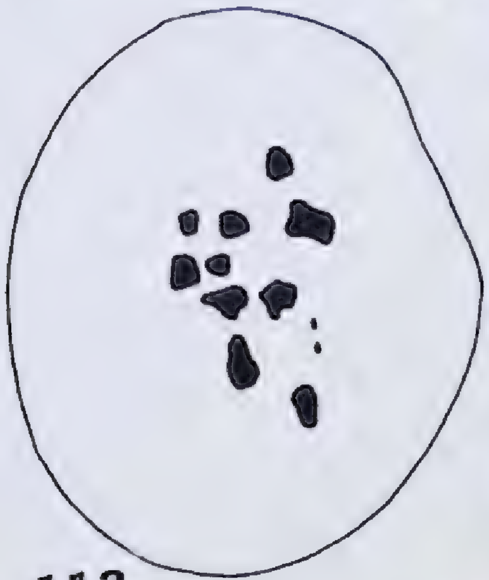
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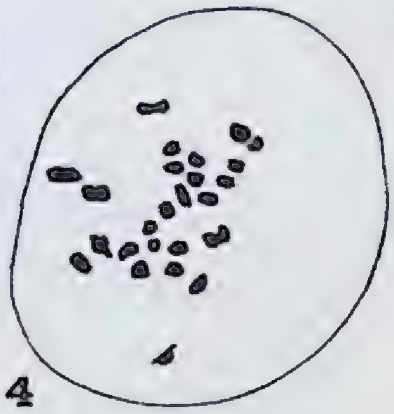
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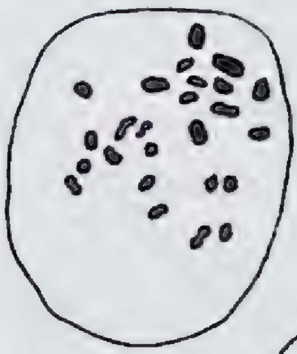
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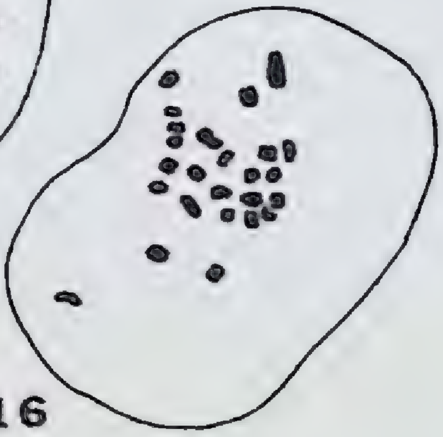
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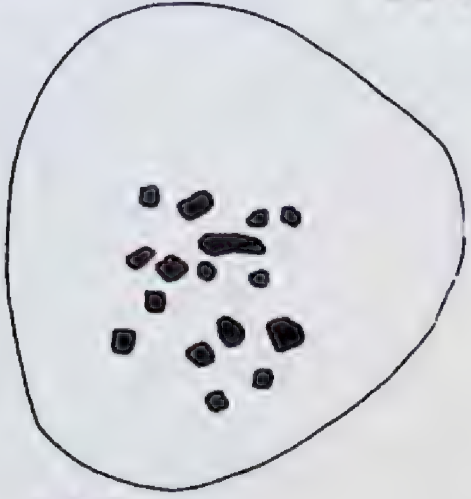
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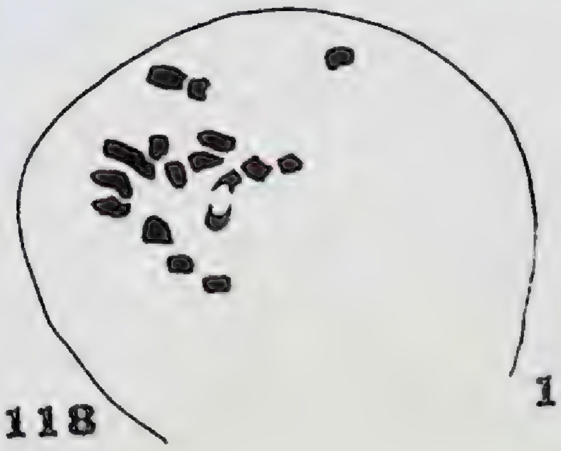
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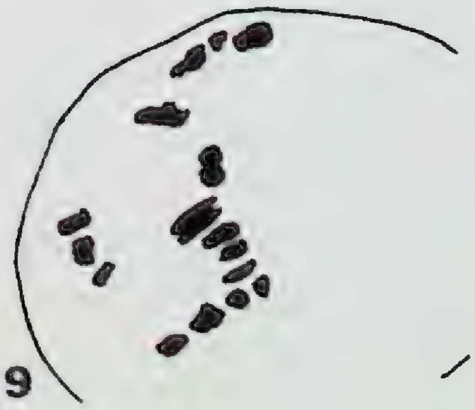
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Figures 120, 121. *Hypnum revolutum* (Mitt.) Lindb., n=14; polar and side views respectively of MI, each showing 14 bivalents.

Figures 122–125. *Isopterygium pulchellum* (Hedw.) Jaeg., n=11, n=22; figs. 122–124, polar views of MI from 11-chromosome population; two bivalents have already disjoined; fig. 125; polar view of MI of 22-chromosome population.

Figures 126–129. *Ptilium crista-castrensis* (Hedw.) DeNot., n=10+1, 2n=20; fig. 126, 127, polar views of somatic metaphase from sporogenous tissue of young capsules, showing 20 somatic chromosomes, the diploid complement; fig. 128, side view of MI, with 10 large bivalents and one small bivalent shown; the small bivalent is in the process of disjunction; fig. 129, polar view of MI; the small bivalent has separated with the two resulting half-bivalents shown.

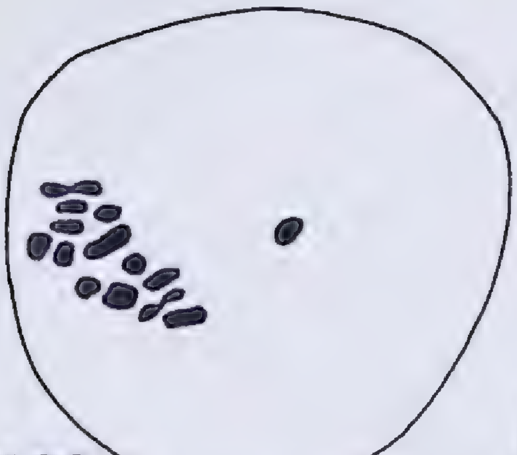
Figure 130. *Pogonatum alpinum* (Hedw.) Röhl., n=7; polar views of MI, showing seven bivalents in each.

Figure 131. *Pogonatum alpinum* var. *septentrionale* (Röhl.) Brid., n=7; polar view of MI with seven bivalents shown in each.

Figure 132. *Polytrichum juniperinum* Hedw., n=7; polar view of MI, showing seven bivalents.

Figure 133. *Polytrichum piliferum* Hedw., n=7; polar view of MI, with seven bivalents shown.

Figures 134, 135. *Polytrichadelphus lyallii* Mitt., n=7; fig. 134; diakinesis, showing seven pairs of chromosomes; fig. 135; polar view of MI, with seven bivalents indicated.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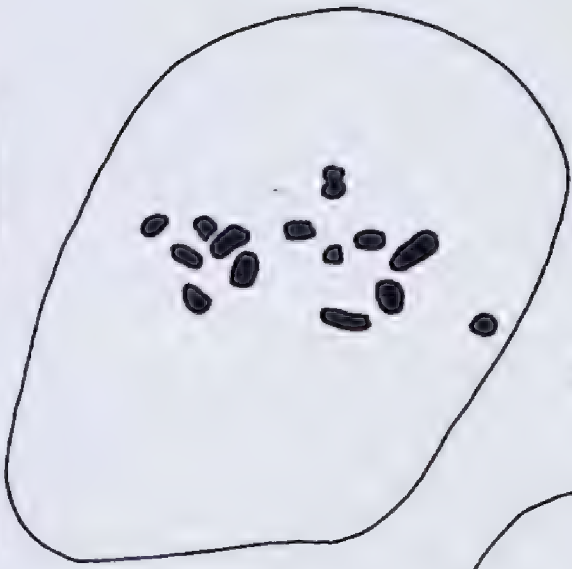
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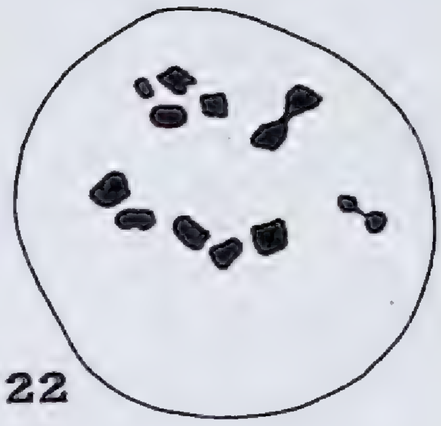
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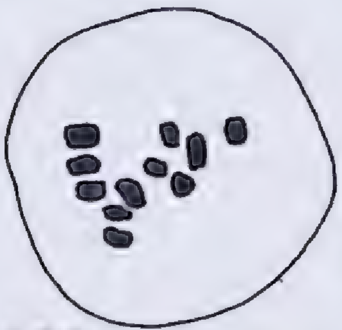
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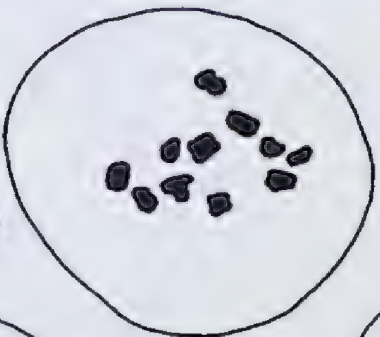
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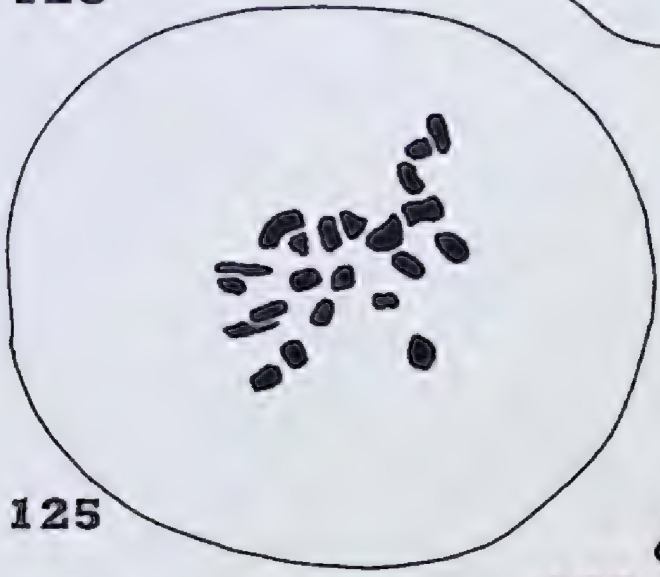
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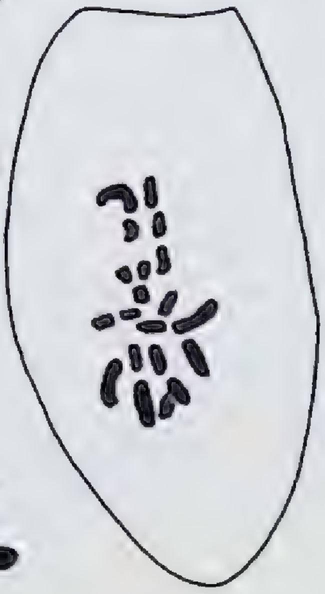
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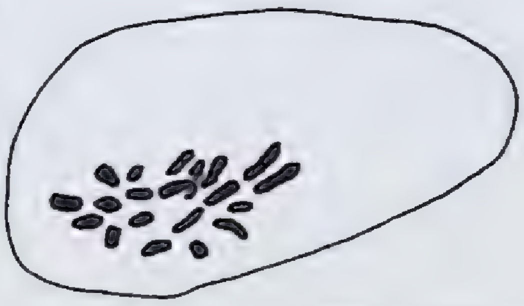
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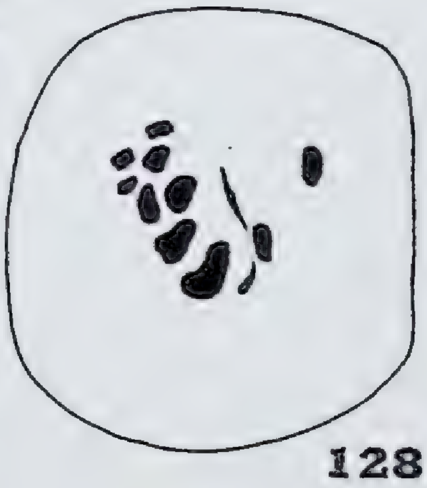
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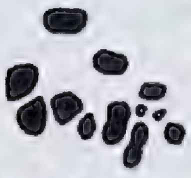
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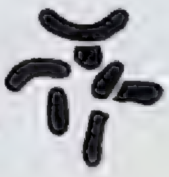
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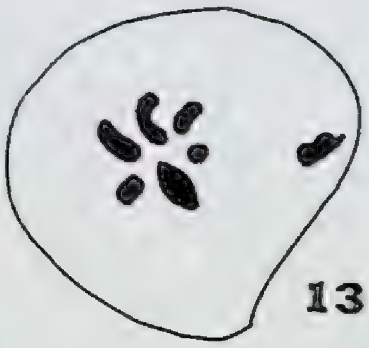
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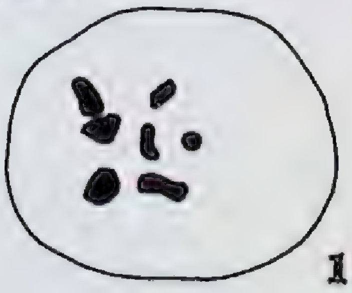
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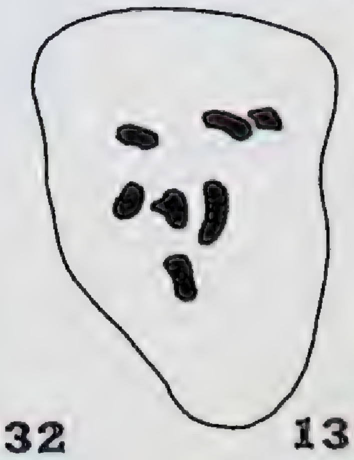
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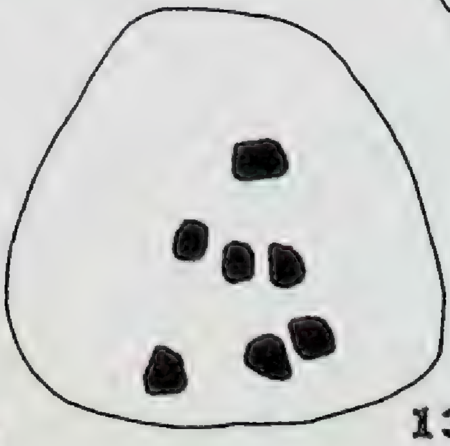
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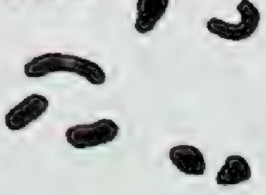

THE MOSSES OF GILLAM, MANITOBA

HOWARD CRUM AND WILFRED B. SCHOFIELD

The boreal coniferous forest is rather uniform in floristic composition. In almost any part of its vast extent across the continent, a high percentage of the same species may be found in similar habitats and associations. For that reason, and also because of difficulties in travelling through northern bush, botanical exploration in Canada has been largely concentrated elsewhere. As a result, distributions of plant species in a great part of the country are known only from reasonable inferences based on very spotty records.

A survey of the meagre literature on bryophytes of the forested North illustrates the point in exaggeration. Few botanists working in the North have had any knowledge of bryophytes or any training in seeking out more selective habitats. Most of the collections recorded in the literature were made incidentally and haphazardly. Only Ritchie's interesting collection of 40 species from northwestern Manitoba was made entirely within the coniferous forest (Ritchie, 1956). The other collections came from very large areas inclusive of vegetational zones other than the boreal coniferous forest. For example, Wynne and Steere's sizable report (1943) includes mosses of the subarctic east coast of Hudson Bay as well as the inland forest. Lepage (1945) listed 115 species from northern Ontario and Quebec, between Lake Mistassini and James Bay, and Kucyniak (1950) reported 70 species from the general vicinity of Lake Mistassini. In 1949 Kucyniak published records of 32 species from the George River District of Quebec. Bartram's paper (1954) includes numerous localities in Ungava and Labrador. None of the reports gives a complete record of the mosses of any one area or a representative sampling of the flora to be expected in similiar areas elsewhere in the boreal forest.

The present report of mosses collected in northern Manitoba is interesting for two reasons: *first*, it is the only reasonably complete record of mosses found in a small area wholly within the boreal coniferous forest; and, *second,* it includes a number of supposedly rare and local species whose presence there could not have been inferred from their known distributions elsewhere.

In August of 1956 the senior author collected bryophytes intensively during a short stay at Gillam, at Mile 326 on the Hudson Bay Railway. The junior author had also collected there during a period of three months in 1950, when he was employed by the Department of Agriculture on an entomological survey. By combining records of both collections, it is possible to present a list of 108 species and nine varieties of mosses for an area extending some 12 or 13 miles along the railway and including Gillam and the nearby Kettle River, Kettle Rapids (on the Nelson River about six miles from Gillam), and Sky Pilot Creek (12 miles from Gillam at Mile 338).

As expected, most of the mosses are common and widespread in the North. Some, however, are reported as range extensions of considerable note: *Cinclidium latifolium* and *Bryum acutum* were previously known only as rarities of high arctic latitudes; *Bryum longisetum* was known from two collections, in Labrador and the Yukon; *Mnium andrewsianum,* only recently described as a new species, is now known from many scattered localities from Greenland to Alaska and one in Siberia; *Cynodontium alpestre,* apparently rare, has recently turned up in a number of scattered boreal areas; *Orthotrichum pallens* var. *parvum, Mniobryum atropurpureum,* and *M. vexans* are interesting disjuncts from the West; *Plagiothecium laetum* seems to be an essentially temperate species at or near their northern limits; *Drepanocladus exannulatus* var. *brachydictyus* fo. *tundrae,* now generally recognized in Europe at the specific level, and *Calliergon richardsonii* are probably rather common in the North but not often reported in the literature. Many other records of interest fill in the exceedingly inadequate statements of range given in Grout's *Moss Flora of North America.*

Ecological Considerations

The altitude at Gillam is only 453 feet above sea-level, and the surrounding country is relatively low in topography. Kettle River follows a tortuous course among gravelly hills of glacial origin. Numerous streamlets cut through willow-alder thickets to the river. Lakes are few, but many permanent pools are found in the lowlands where temporary pools are a conspicuous feature in the spring. Glacial till (consisting largely of calcareous silt, clay, and pebbles, as well as scattered granitic boulders) underlies most of the area. Quartzite rocks outcrop only at Kettle Rapids.

The characteristic association of the area is a dense spruce-larch forest in which *Picea mariana* and *Larix laricina* share dominance, except in wetter, more peaty habitats where *Larix* is more abundantly represented. The shrubby vegetation consists of several species of willow (*Salix myrtillifolia, S. vestita, S. bebbiana, S. planifolia,* etc.), *Betula glandulosa, Vaccinium uliginosum, Ledum groenlandicum,* and *Rosa acicularis* (*s. lato*); the most common creeping shrubs are *Vaccinium vitis-idaea* var. *minus, Empetrum nigrum* var. *hermaphroditum,* and *Arctostaphylos alpina.* Herbs are scattered and include, most notably, *Mitella nuda, Equisetum sylvaticum* and *E. palustre, Orchis rotundifolia, Carex vaginata, Linnaea borealis* var. *americana, Polygonum viviparum, Rubus acaulis, Geocaulon lividum,* and *Habenaria obtusata.* The damp humus of the forest floor supports *Hylocomnium splendens* and *Aulocomnium palustre* in quantity, and various species of *Dicranum* are common. In springy places *Sphagnum* or *Tomenthypnum* mats are luxuriantly developed, and around small pools *Cinclidium stygium* and various species of *Drepanocladus* and *Calliergon* are abundantly represented. On wet humus, twigs, and branches on the forest floor, *Distichium capillaceum, Amblystegiella sprucei, Campylium hispidulum* var. *sommerfeltii,* and *Isopterygium pulchellum* are common.

An open spruce-pine (*Picea mariana-Pinus banksiana*) forest forms a transition between the wet lowland forest and the jack pines of dry uplands. Both fruticose and foliose lichens grow abundantly on the forest floor, and such mosses as *Hylocomium splendens, Pleurozium schreberi, Drepanocladus uncinatus,* and *Ceratodon purpureus* are conspicuous. Both *Tetraplodon mnioides* and *T. angustatus* are occasional on the dung of carnivores. Flowering plants are scattered and include species characteristic of both the spruce-larch and the jack pine forests, but *Viola renifolia* and *V. adunca, Fragaria vesca, Achillea millefolium* (*s. lato*); *Petasites palmatus, Ribes oxycanthoides,* and *Cornus canadensis* are more common here than elsewhere in the area.

An open jack pine (*Pinus banksiana*) forest occupies dry hilltops. *Picea mariana* is occasionally encountered in association with the pines; *Picea glauca* is even more rare. The forest floor is covered mainly with fruticose lichens in dense and extensive mats. The moss flora is extremely poor. Flowering plants include such heliophytes as *Vaccinium vitis-idaea, Arctostaphylos uva-ursi, Linnaea borealis* var. *americana, Epilobium angustifolium, Anemone multifida, Potentilla tridentata, Geocaulon lividum,* and *Oryzopsis pungens.* Occasional shrubs are *Vaccinium myrtilloides, Ledum groenlandicum,* and *Rosa acicularis (s. lato).*

On dry sandy hilltops *Betula papyrifera* var. *neo-alaskana* forms sparse, open stands. Clones of *Populus balsamifera* or *P. tremuloides* are frequently intermingled with the birch and sometimes replace it. Shrubs are abundant and include *Rosa acicularis, Amelanchier alnifolia, Viburnum edule, Juniperus communis* var. *depressa, Cornus alternifolia,* and *Prunus pensylvanica.* The herbaceous flora includes a number of species not found in other habitats: *Anemone multifida, Aquilegia brevistyla, Geranium bicknellii, Phacelia franklinii, Carex backii, C. deflexa,* and *C. houghtonii.* The mosses are few and include *Ceratodon purpureus, Polytrichum juniperum, P. piliferum,* and *Abietinella abietina.*

Granitic boulders are scattered throughout the woodlands. *Hedwigia ciliata, Grimmia affinis, G. alpicola,* and, rarely, *Andreaea rupestris* grow on them. The quartzite outcrops along the Nelson River support a phanerogamic flora conspicuously different from that of the rest of the area. On the quartzite outcrop on the bank of Nelson River at Kettle Rapids, the rock-crevices, damp depressions, and deep rock-pools provide habitats for a different phanerogamic and cryptogamic flora. Here are found the following plants, rare or absent elsewhere in the area: (a) in the rock crevices and damp depressions—*Castilleja raupii, Elaeagnus argentea, Arnica wilsoni, Solidago graminifolia* var. *major, Aster praealtus, Lathyrus palustris,* and *Thalictrum confine,* among others; (b) in the rockpools—*Ranunculus reptans, Eleocharis smallii, Callitriche hermaphroditica,* and *Utricularia vulgaris.* Among the bryophytes, several species of *Grimmia, Orthotrichum anomalum, O. pallens* var. *parvum, O. speciosum* var. *elegans, Tortula norvegica, Leskeella nervosa,* and *Pylaisia polyantha* were found there on dry rocks or on thin soil, and *Barbula fallax, Philonotis fontana, Bryum acutum,* and *Mniobryum wahlenbergii* grew on wet soil in rock depressions.

Sphagnum bogs are uncommon and never very large, except near the village where clearing and burning have created an extensive area of open bogs and sedge meadows. *Sphagnum fuscum, S. capillaceum* var. *tenellum, S. warnstorfianum, Dicranum bergeri, Aulacomnium palustre,* and *Polytrichum juniperinum* var. *alpestre* are particularly common mosses in the bogs, and in places where sedges grow among the *Sphagnum* hummocks (presumably less acid), *Paludella squarrosa* and *Meesia uliginosa* are well represented. *Carex aquatilis, C. canescens,* and *Eriophorum spissum* are common on the *Sphagnum* mat. At the bog margins, characteristic flowering plants are *Smilacina trifolia, Rubus chamaemorus, Chamaedaphne calyculata, Ledum groenlandicum, Kalmia polifolia, Vaccinium oxycoccus, V. uliginosum, V. vitis-idaea* var. *minus, Empetrum nigrum, Salix candida,* and *S. pedicellaris* var. *hypoglauca.*

Sphagnum hummocks are also found on gentle seepage slopes in the spruce-larch forest. *Vaccinium oxycoccus, V. vitis-idaea* var. *minus,* and *Pinguicula villosa* grow in close association with the *Sphagnum,* and large clumps of *Polytrichum juniperinum* var. *alpestre* are very common here. The hummocks are often encrusted with a limy deposit, and small pools among the hummocks are often bordered by *Catoscopium nigritum,* usually a pronounced calciphile, as well as *Dicranum bergeri* and *Tomenthypnum nitens* in dense mats, and such herbs as *Carex capillaris, C. scirpoidea, Polygonum viviparum,* and *Equisetum sylvaticum.* On some slopes, *Eriophorum spissum, Scirpus cespitosus* var. *callosus, Triglochin maritima, T. palustris, Juncus balticus, J. castaneus, J. albescens, Tofieldia pusilla,* and *T. glutinosa* are found in abundance.

Many of the more interesting mosses grow on disturbed soil where they flourish briefly as pioneers before being crowded out by competition. Such habitats as sheltered banks beneath projecting sods are found along the railroad track and the few primitive roads in the area, around the roots of fallen trees and particularly on the exposed limy till of the bluffs above Kettle River. In these habitats may be found *Dicranella grevilleana, D. varia, Encalypta rhabdocarpa, E. procera, Tortula mucronifolia, Aloina brevirostris,* and *Bryum pallescens,* as well as less restricted species such as *Distichium capillaceum* and *Myurella julacea. Catoscopium nigritum* is common on wet clay along the railway. A number of weedy species, *Ceratodon purpureus, Barbula convoluta, Leptobryum pyriforme, Bryum argenteum, B. cuspidatum,* and *Funaria hygrometrica,* may be found easily on disturbed soil.

Drepanocladus swamps are rather common in the lower woodlands where mats of *D. aduncus, D. exannulatus, D. revolvens, Calliergon giganteum, C. sarmentosum, Scorpidium scorpioides,* and *Tomenthypnum nitens* encroach on shallow ponds and sometimes fill them. Growing on such mats are numerous phanerogams rarely found elsewhere: *Salix candida, Menyanthes trifoliata* var. *minor, Caltha palustris, Cardamine pratensis, Carex limosa, Agrostis scabra, Eriophorum viridi-carinatum, Epilobium palustre, Equisetum palustre, E. fluviatile, Galium palustre, Cicuta bulbifera, Potentilla palustris, Rumex fenestratus, Habenaria hyperborea, Salix pedicellaris* var. *hypoglauca, Viola palustris,* and many others. The wet sedge meadows at the borders of such swamps are rich in such mosses as *Paludella squarrosa, Meesia triquetra, Aulacomnium palustre, Helodium blandowii,* and *Campylium stellatum,* as well as *Tomenthypnum, Scorpidium,* and species of *Drepanocladus* and *Calliergon.*

In the lowlands, small streams are generally canopied by thickets of alders (both *Alnus crispa* and *A. rugosa*) and many species of willow. *Climacium dendroides* and *Mnium affine* are common and characteristic in such places, otherwise of little bryological interest. Typical phanerogams include *Lonicera involucrata, Actaea rubra, Ribes hudsonianum, Viola renifolia* var. *brainerdii, Viburnum edule,* and *Glyceria striata.*

Other habitats of little bryological interest are two lakes, the larger of which has a sandy bottom and contains no mosses, and the river margins, which have no characteristic bryophyte floras except on sheltered bluffs and rock outcrops, as described above.

In the following list no attempt was made to cite all the collections of less interesting species. Numbers preceded by *"S"* represent specimens collected by Schofield. They were originally named by Dr. William C. Steere and are kept in the Herbarium of the Department of Agriculture in Ottawa. Determinations were checked in every case. Numbers preceded by *"C"* were collected by Crum, whose specimens are deposited in the herbarium of the National Museum of Canada.

SPHAGNACEAE

Sphagnum capillaceum (Weiss) Schrank. Gillam (*S*–1253). Kettle Rapids (*C*–7557). In spruce and spruce-larch stands. Var. *tenellum* (Schimp.) Andr. Gillam (*S*-1251; *C*-7458). Kettle Rapids (*C*-7552). In an open peat bog and also in spruce and spruce-larch stands.

Sphagnum fuscum (Schimp.) Klinggr. Gillam (*C*–7430; *C*–7471). In open peat bogs.

Sphagnum recurvum P.B. Gillam (*S*-1289; *S*-1252 *p.p.,* with *S. squarrosum*). In moist spruce-larch forests.

Sphagnum riparium Ångstr. Gillam (C-7402). In *Eriophorum* bog.

Sphagnum squarrosum Crome. Gillam (*S*-1252). Wet margin of spruce-larch forest.

Sphagnum warnstorfianum DuRietz. Gillam (*C*-7360; *C*-7410; *C*-7448; *C*-7512). In a wet sedge meadow, open peat bog, and also spruce muskeg.

ANDREAEACEAE

Andreaea rupestris Hedw. Gillam (*S*-843; *S*-984). In crevices of granitic boulders.

DITRICHACEAE

Ditrichum flexicaule (Schwaegr.) Hampe. Gillam (*C*-7447; *C*-7518; *S*-1448). On humus on floor of dry spruce forest, in a moist depression in a spruce-larch stand and in seepage near base of sandy hill. Var. *densum* (BSG) Braithw. Gillam (*C*-7453). On gravelly soil of roadbank.

Saelania glaucescens (Hedw.) Broth. Sky Pilot Creek (S-1113). Gillam (S-1180). On damp soil of protected bank.

Ceratodon purpureus (Hedw.) Brid. Gillam (*C*-7388; *C*-7425; *C*-7433). On soil of paths and bank along railway; common and weedy.

Distichium capillaceum (Hedw.) BSG. Gillam (*C*-7385; *C*-7434; *C*-7487). On moist, shaded soil of banks and also on sides of a hole in the floor of a damp spruce forest.

Distichium inclinatum (Hedw.) BSG. Gillam (*C*-7358; *C*-7383). On the base of a dead willow in an open peat bog and on side of a tussock in a wet sedge meadow.

DICRANACEAE

Dicranella grevilleana (Brid.) Schimp. Gillam (*C*-7530; *S*-847). On moist, shaded soil and humus of banks. —"Idaho, Montana, Washington and north to Behring Sea" (Grout, 1928-40). This species has also been found at Churchill, Manitoba; Steere (1937) reported it from Keweenaw Co., in northern Michigan; and we have specimens at the National Museum of Canada from New Brunswick, Anticosti Island, and Gaspé.

Dicranella varia (Hedw.) Schimp. Gillam (*C*-7488; *S*-864 *p.p.*, with *Moerckia hibernica*). On damp, disturbed soil.

Cynodontium alpestre (Wahl.) Lindb. Gillam (*C*-7499). On shaded humus of bank. —These plants compare very well with the type collection of *C. strumulosum* C.M. & Kindb. from Hector, British Columbia. Dr. Herman Persson has recently found that *C. strumulosum* is a synonym of *C. alpestre*, a species otherwise known from several places in Alaska (see Persson & Weber, 1958), Newfoundland (Persson, in litt.) and Greenland (Grout, 1928–40). It is very common at Churchill and is very likely common elsewhere throughout subarctic Canada but previously overlooked because of its small size.

Cynodontium strumiferum (Hedw.) Brid. Gillam (*S*-992). In crevices of an igneous boulder.

Oncophorus virens (Hedw.) Brid. Gillam (*C*-7405). On a damp, rotted twig on the floor of a spruce forest.

Oncophorus wahlenbergii Brid. Gillam (*C*-7405 *p.p.*, with *O. virens*). As above.

Dicranum bergeri Bland. Gillam (*C*-7446; *C*-7497; *S*-1488). Kettle Rapids (*C*-7541). On shaded humus in spruce forests and on the sides of old *Dicranum* and *Sphagnum* tussocks in open peat bogs.

Dicranum bonjeanii DeNot. Gillam (*S*-1447). On moist portions of railroad right-of-way.

Dicranum fuscescens Turn. Gillam (*C*-7468). On dry humus in the shade of a spruce tree.

Dicranum groenlandicum Brid. Gillam (*C*-7406). Forming a tussock on the floor of a spruce forest.

Dicranum muehlenbeckii BSG. Gillam (*C*-7420; *S*-1481). On humus in dry spruce forests.

Dicranum rugosum Brid. Gillam (*C*-7416). On humus in a dry spruce forest.

ENCALYPTACEAE

Encalypta procera Bruch. Gillam (*C*-7421; *S*-1468). On a gravelly roadbank and on humus over a hummock.—The range given in Grout's *Moss Flora* (1928–40) is quite inadequate. In addition to "Alaska to Montana, Idaho and Washington," which includes both British Columbia and parts of Alberta, one can add Churchill, Manitoba, southern Yukon, and the following Canadian Eastern Arctic localities recorded in the literature: Ellesmere and North Kent Islands (Bryhn, 1906–07), Cornwallis Island (Steere, 1951), and Prince Patrick Island (Steere, 1955). The National Museum of Canada has specimens from Port Arthur and Lake Nipigon, Ontario.

Encalypta rhabdocarpa Schwaegr. Gillam (*C*-7452). On a gravelly roadbank. "British Columbia, Alaska, Montana, California, Idaho, Colorado, Ontario" (Grout, 1928–40). The species is also common at Churchill, the Rocky Mountains, in Alberta, and in southern Yukon. John Macoun found it in the Cypress Hills of Saskatchewan, and his son, J. M. Macoun, collected it at "Clearwater River, N.W.T.," either in northern Alberta or Saskatchewan (specimens in Nat. Mus. of Canada). It has been reported from northern Quebec (Wynne & Steere, 1943), Cornwallis Island (Steere, 1951), Baffin Island (Steere, 1941), Melville Peninsula (Steere, 1941), and Prince Patrick Island (Steere, 1955). Furthermore, Steere (1948) listed many other records from the Canadian Eastern Arctic and stated that this is the most common species of the genus in that vast area.

POTTIACEAE

Weissia controversa Hedw. Gillam (*C*-7480). Kettle Rapids (*S*-910). On wet clay.

Tortella fragilis (Drumm.) Limpr. Gillam (*C*-7469; *C*-7518 *p.p.*, with *Ditrichum flexicaule*). On damp, exposed, disturbed soil and on humus in a damp depression in the floor of a spruce-larch forest.

Barbula convoluta Hedw. Gillam (*C*-7519). On disturbed gravel near railway.

Barbula fallax Hedw. Kettle River (*S*-891). On muddy soil near river.

Bryoerythrophyllum recurvirostrum (Hedw.) Chen. Gillam (*C*-7503); Kettle Rapids (*S*-1479). On damp, shaded side of an old *Sphagnum* hummock and on soil in rock crevice.

Aloina brevirostris (Hook. & Grev.) Kindb. Gillam (*S*-1129; *S*-1326). On calcareous soil; No. 1326 came from dried limestone mud on the roof of an icehouse. Steere (1950) has mapped the North American distribution of this interesting boreal species, which occurs in suitable habitats across the continent. It can also be recorded from many localities in southern Yukon, Banff and Jasper parks, and Nipigon, Ontario; it is almost invariably a pioneer on calcareous silt banks or on limy soil of disturbed places. (Eastern American reports of *Aloina rigida* can almost surely be referred here.)

Tortula mucronifolia Schwaegr. Gillam (*C*-7525; *S*-1455). On gravelly roadbank and damp sandy soil near river.

Tortula norvegica (Web.) Kindb. Kettle Rapids (*C*-7551; *C*-7555; *S*-908). On thin soil covering dry rocks and in rock crevices.

GRIMMIACEAE

Grimmia affinis Hornsch. Gillam (*S*-1368). Kettle Rapids (*S*-931). In crevices of boulders.

Grimmia alpicola Hedw. Gillam (S-900). Kettle Rapids (S-914; *S*-917; *S*-918; *S*-920; *S*-924; *S*-928; *S*-933; *S*-935; *S*-1544). In crevices of boulders. Var. *rivularis* (Brid.) Broth. Kettle Rapids (*C*-7540). On a rock near the river.

Grimmia apocarpa Hedw. Gillam (*S*-1482). Kettle Rapids (*S*-913; *S*-919). On rocks near river.

FUNARIACEAE

Funaria hygrometrica Hedw. Gillam (*S*-1009). On damp, disturbed sand; common and weedy.

SPLACHNACEAE

Tetraplodon angustatus (Hedw.) BSG. Gillam (*C*-7400). On dung of carnivore, dry floor of a spruce forest.—"Newfoundland, Cape Breton, Ontario, Athabasca, British Columbia, Rockies, Minnesota, Catskills, Adirondacks" (Grout, 1928–40). Many more localities could be cited for this boreal species. It is common at moderate altitudes, in dry spruce forests, in the Rocky Mountains of British Columbia and Alberta, and in similar situations in southern Yukon. It has also been collected at Bonanza Creek near Dawson, Y.T., near Churchill and at Lake Winnipegosis, Man., and also in New Brunswick and in Vermont (Specimens all at the National Museum of Canada). The senior author has collected it near Fairbanks, Alaska, and Persson (1954) recorded another collection from the same area. Sherrard (1957) reported finding it in the Mt. McKinley region.

Tetraplodon mnioides (Hedw.) BSG. Gillam (*C*-7401). On dung of a carnivore in the dry floor of a spruce forest.

Splachnum ovatum Hedw. Gillam (*S*-1440). On animal waste.

BRYACEAE

Pohlia cruda (Hedw.) Lindb. Gillam (*C*-7427 *p.p.*, with *P. nutans*, *S*-1483 *p.p.*, with *Eurhynchium pulchellum*). On damp shaded side of old *Sphagnum* hummock and on moist soil of river-bank.

Mniobryum atropurpureum (Wahl.) Hag. Kettle River (*S*-889). On mud of river-bank.—"In America found in the northwest, from British Columbia to Montana and North Dakota" (Grout, 1928–40).

Mniobryum vexans Limpr. Gillam (*C*-7531). On moist, shaded soil.—Montana, Idaho, northern Alberta, and British Columbia (Grout 1928–40). This species has a rather characteristic appearance when dry so that sterile specimens, such as this one, can be named with reasonable certainty; Dr. A. LeRoy Andrews has confirmed the determination as most probably correct. Persson and Weber (1958) reported the species from the Mt. McKinley region of Alaska.

Mniobryum wahlenbergii (Hedw.) Jenn. Kettle Rapids (*C*-7547). On wet soil over rock near the river.

Leptobryum pyriforme (Hedw.) Schimp. Gillam (*C*-7396; *C*-7513; *C*-7532; *S*-1446). On damp, disturbed soil, in spruce forest and also on exposed banks along railroad, etc.

Bryum acutum Lindb. Kettle Rapids (*S*-1486; *S*-1490). In wet crevices and depressions of rocks near river. A very rare species in arctic America, known from a few stations from Greenland to Alaska.

No. 1486 is well developed and compares fairly well with European specimens of *B. acutum* and *B. acutiforme,* a supposed synonym, but the inner peristome adheres to the exostome, and the cilia, though rudimentary, are more evident than in those specimens. In a letter, July 4, 1958, Dr. A. LeRoy Andrews said: "I do not think it is *B. acutum*. . . .It seems to me to be in the relationship of *B. arcticum,* but like yourself I found it autoicous where *B. arcticum* has been consistently synoicous, and it has other points of difference from the latter species. I doubt if it fits any of the species that I have credited to North America, and unless I can find something else among the many described European species, it may prove new." On July 29, 1958, he wrote further: "The *Bryum* . . . I am now disposed to think is *B. purpurascens*. It is not *acutum* and not *arcticum*. There may be slight differences from the European and eastern American *purpurascens,* and I am not yet finished with the matter, but this is the nearest I can get at present." This problem obviously deserves further study; the fact that the inflorescence is autoicous would seem to rule out *B. purpurascens,* in spite of many points of similarity.

Bryum argenteum Hedw. Gillam (*S*-1393). Kettle Rapids (*S*-909). On limy soil on the roof of an icehouse and in crevices of an igneous rock near the river.

Bryum blindii BSG. Gillam (*C*-7422). On damp, gravelly clay, disturbed, in spruce forest.—At the National Museum we have three collections from the Thunder Bay District of Ontario and two from the Rocky Mountains of British Columbia. (Dr. Herman Persson kindly supplied the determination for this specimen.)

Bryum cuspidatum (BSG) Schimp. Gillam (*C*-7412; *C*-7514; *C*-7807). On wet, shaded gravel in railway ditch, on the wet base of a dead willow and also on a damp shaded peat bank.

Bryum longisetum Bland. Gillam (*C*-7419). In a damp depression in a fairly dry spruce muskeg.—Previously known only from Dawson (Yukon) and Labrador (Grout, 1928–40).

Bryum pallens (Web. & Mohr) Brid. Gillam (*C*-7422 *p.p.*, with *B. blindii*). On damp gravelly clay, disturbed, in spruce forest. Dr. Herman Persson identified this species. The plants are sterile, but compare well with authentic material.

Bryum pallescens Schleich. Kettle River (*S*-1313). On damp soil near the river.

Bryum pseudotriquetrum (Hedw.) Schwaegr. Gillam (*C*-7366; *C*-7373; *C*-7395; *C*-7521). Kettle River (*S*-1156). Kettle Rapids (*S*-1371). On wet soil of river-bank, in swamps and sedge meadows, and also in an open peat bog on the wet base of a stump.

MNIACEAE

Mnium affine Bland. Gillam (*C*-7415; *C*-7470; *C*-7481). On wet soil under willows and in spruce muskeg. These plants show a poor development of marginal teeth on the leaves and may be referred to the segregate species, *M. rugicum* Laur.

Mnium andrewsianum Steere. Gillam (*C*-7522). In a wet shaded depression in a spruce forest. This species, very recently described by Steere (1958), was recently reported as an undescribed species by Ritchie (1956) from northwestern Manitoba. It is common at Churchill and has been found in many scattered localities from Greenland to Siberia (Steere, 1958).

Cinclidium latifolium Lindb. Gillam (*C*-7443; *C*-7509). On wet soil and humus in a spruce muskeg and in its swampy margin.—This is a remarkable range extension of a species which Steere recently considered one of the small group of truly arctic mosses; it is fairly common in the wet tundra at Churchill. For the distribution elsewhere, see Steere's interesting map (1953).

Cinclidium stygium Sw. Gillam (*C*-7368; *C*-7387; *C*-7440; *C*-7449; *C*-7454; *C*-7523). On wet soil and humus in swamps, sedge meadows, and spruce muskeg.

AULACOMNIACEAE

Aulacomnium palustre (Hedw.) Schwaegr. Exceedingly common in open peat bogs, spruce forest and muskeg, swamps and sedge meadows.

MEESIACEAE

Paludella squarrosa (Hedw.) Brid. Gillam (*C*-7365; *C*-7467). In a wet sedge meadow and among sedges in an open burned-over peat bog.

Meesia triquetra (Hook. & Tayl.) Ångstr. Gillam (*C*-7365; *C*-7467). In wet sedge meadow and among sedges in an open, burned-over peat bog.

Meesia uliginosa Hedw. Gillam (*C*-7391; *C*-7380; *C*-7528; *S*-1059; *S*-1297; *S*-1382). On humus in wet sedge meadows, open peat bogs and spruce-larch woods.

CATOSCOPIACEAE

Catoscopium nigritum (Hedw.) Brid. Gillam (*C*-7491; *S*-842; *S*-1309). On wet clay.—Common in parts of the Canadian Rockies, particularly near Jasper, Alberta, at Churchill, and in southern Yukon, this calciphilous species probably ranges throughout boreal and arctic North America where edaphic conditions are favourable. Grout (1928–40) said, "This plant is rather rare and seems to be more frequent in the Great Lakes region and the Rocky Mts.; Alaska, British Columbia, Montana." Steere (1948) cited collections from Ellesmere, North Kent, and Baffin islands and elsewhere reported the species from Churchill and the Melville Peninsula (1941), Cornwallis Island (1951), and Prince Patrick Island (1955). Steere and Wynne (1943) recorded it from the Belcher Islands. Persson and Gjaerevoll (1957) listed several floristic divisions of Alaska in which it has been found: Aleutian Islands, Bering Strait, Arctic Coast, Alaska Range, and Central Yukon River.

BARTRAMIACEAE

Philonotis fontana (Hedw.) Brid. Kettle Rapids (*C*-7543). On wet soil among rocks on the river-bank.

ORTHOTRICHACEAE

Orthotrichum anomalum Hedw. Kettle Rapids (*S*-915). In rock crevices.

Orthotrichum obtusifolium Brid. Gillam (*S*-1484). On bark at base of *Populus balsamifera*.

Orthotrichum pallens var. *parvum* Vent. (*det. ex char.*) On side of granite boulder, Kettle Rapids of Nelson River, near Gillam (*S*-1543).—No authentic material has been available for study, and, therefore, this report is somewhat questionable. The species proper is not definitely known to occur in North America, and this variety is known otherwise only from Wyoming and Utah.

Orthotrichum speciosum var. *elegans* (Hook. & Grev.) Warnst. Gillam (*S*-886; *S*-1181). Kettle Rapids (*S*-929; *S*-934). On dead twigs of trees, wood litter, and also on the moist side of a boulder.—This variety is not very distinct from *O. speciosum*, although the capsules are only striated occasionally, and then when quite old; it can be segregated fairly well by major area, although the ranges overlap somewhat. (Numerous specimens from Churchill seem to belong to the species proper.) "Northern United States and southeastern Canada, mostly east of the Mississippi" (Grout, 1928–40).

CLIMACIACEAE

Climacium dendroides (Hedw.) Web. & Mohr. Gillam (*C*-7476). On wet humus under a willow.

FONTINALACEAE

Fontinalis duriaei Schimp. Gillam (*S*-1445). In water of a trickle.

HEDWIGIACEAE

Hedwigia ciliata (Hedw.) P-B. Kettle Rapids (*C*-7550). On rock.

THELIACEAE

Myurella julacea (Schwaegr.) BSG. Gillam (*C*-7434 *p.p.*, with *Distichium capillaceum; C*-7472; *C*-7485). On damp, shaded soil and humus on banks.

LESKEACEAE

Leskeella nervosa (Schwaegr.) Loeske. Kettle Rapids (*C*-7554; *S*-911). On rocks on the river-bank and in the nearby woods.

THUIDIACEAE

Abietinella abietina (Hedw.) C.M. Gillam (*S*-877). On sandy soil.

Thuidium recognitum (Hedw.) Lindb. Gillam (*S*-1535). In wet spruce-larch woods.

Helodium blandowii (Web. & Mohr) Warnst. Gillam (*C*-7356; *C*-7370). In wet sedge meadows.

AMBLYSTEGIACEAE

Amblystegium serpens (Hedw.) BSG. Gillam (*S*-1542). On stick of wood in spruce forest.

Campylium chrysophyllum (Brid.) Bryhn. Gillam (*S*-1448 *p.p.*, with *Ditrichum flexicaule; S*-1456; *S*-1468 *p.p.*, with *Encalypta procera*). On humus over a hummock, on a decaying log, and in seepage near base of a sandy hill.

Campylium hispidulum var. *sommerfeltii* (Myr.) Lindb. Gillam (*C*-7398 *p.p.*, with *Amblystegiella sprucei; C*-7472 *p.p.*, with *Myurella julacea; C*-7508). On wet, shaded humus in spruce forests.

Campylium polygamum (BSG) Bryhn. Gillam (*C*-7479). In a depression in a dryish, open peat bog.

Campylium stellatum (Hedw.) Lange & C. Jens. Gillam (*C*-7361; *C*-7375). On wet soil of a sedge meadow and also on the damp bank of a railway ditch.

Drepanocladus aduncus (Hedw.) Warnst. Gillam (*C*-7496). In a dried-up bog near the lake. Var. *polycarpus* fo. *gracilescens* (BSG) Moenk. Gillam (*C*-7363; *C*-7378; *C*-7389). In wet sedge meadows and at the margin of a swamp.

Drepanocladus exannulatus (BSG) Warnst. Gillam (*C*-7507; *C*-7536). In wet places, at the edge of a pool and in a depression in an open peat bog. Var. *brachydictyus* fo. *tundrae* (Arn.) Moenk. Gillam (*C*-7387 *p.p.*, with *Cinclidium stygium; C*-7537). In seepage at edge of a swamp and also at the margin of a pool.—Recorded by Grout only from Dawson in the Yukon, this distinctive form has also been found at Churchill. In view of the fact that *Drepanocladus exannulatus* is highly polymorphous and includes many odd extremes, it seems that even this form, so striking and so suggestive of *Calliergon sarmentosum,* ought not to be dignified by recognition at the specific level unless it can be demonstrated to be more than a habitat expression (as most of the other variations in the complex doubtless are). Persson (1952) gave several American localities for *D. tundrae,* and additional records for Alaska were reported by Sherrard (1957), Persson and Gjaerevoll (1957), and Persson and Weber (1958).

Drepanocladus revolvens (C.M.) Warnst. Gillam (*C*-7364; *C*-7367; *C*-7379; *C*-7408; *C*-7441; *C*-7494). Common in wet sedge meadows and in wet depressions in spruce muskegs.—Most of the local collections could be segregated as *D. intermedius* (Lindb.) Warnst., which is the more common form encountered in Canada, but it is quite variable and is scarcely differentiated except in colour from *D. revolvens.*

Drepanocladus uncinatus (Hedw.) Warnst. Gillam (*C*-7428; *C*-7529; *S*-1464; *S*-1493). Kettle Rapids (*S*-1480). On humus, logs and soil in dry spruce forests and among rocks on river-bank. Var. *plumosus* (Schimp.) Ren. Gillam (*C*-7357; *C*-7386). On wet soil in a sedge meadow and under willows in a swamp.

Drepanocladus vernicosus (Lindb.) Warnst. Gillam (*C*-7369). On soil in a wet sedge meadow.

Calliergon giganteum (Schimp.) Kindb. Gillam (*C*-7359; *C*-7404; *C*-7465; *C*-7486; *C*-7502). In wet sedge meadows, under willows in swamps, and in a wet, shaded depression in spruce muskeg.

Calliergon richardsonii (Mitt.) Kindb. Gillam (*C*-7426). In wet spruce muskeg.—"Vermont, Isle Royale . . . and north of Lake Superior, Newfoundland, Prince Edward Island, Greenland" (Grout, 1928–40). This species has been reported from many other parts of the North: Dawson, Yukon (Williams, 1901), Nueltin Lake, Keewatin (Bartram, 1950), northern parts of Labrador and Quebec and Chesterfield Inlet (Steere, 1948), Chesterfield River, Melville Peninsula and Ellesmere Island (Steere, 1941) and Cornwallis Island (Steere, 1941); it has also been found at Churchill. Several Alaskan records are to be found in Persson (1952), Persson and Gjaerevoll (1957), and Persson and Weber (1958).

Calliergon sarmentosum (Mitt.) Kindb. Gillam (*C*-7493). At edge of a pool.—Grout (1928–40) reported that this species is rare and local, known from northern New England, Eastern Canada, Newfoundland, and Greenland. It is actually fairly common in the North and ranges across Canada to the Yukon. Steere (1948) cited collections from nearly every division of the Canadian Eastern Arctic, and this has been confirmed by numerous recent records in the literature. Persson and Gjaerevoll (1957) found it to be fairly common in central Alaska in fens, on river bars, and around springs and snow beds. Records from Mt. McKinley National Park, Alaska, were published by Sherrard (1957) and by Persson and Weber (1958). Steere (1938) reported the species from Little Diomede Island in the Bering Straits.

Calliergon turgescens (Schimp.) Kindb. Gillam (*C*-7489; *C*-7521). In a moist depression in a spruce forest and a dried-up pool in an open peat bog.—Grout considered this to be the rarest of the genus and included only Davis Straits; Rocky Mountains, British Columbia; Owen Sound, Ontario; and Greenland, in its distribution. Wynne (1945) also characterized the species as rare. It is, however, very common in western Alberta in the mountains, in the southern Yukon, and around Churchill. Bryhn (1906–07) referred to it as the most common bog and water moss; Steere (1948) recorded many widespread localities in the Canadian Eastern Arctic, and many other more recent reports from that area could be mentioned. Several Alaskan stations are known (Steere, 1954; Sherrard, 1955; Persson and Gjaerevoll, 1957; Persson and Weber, 1958). It would seem, therefore, that this species, a pronounced calciphile, is to be found across the continent in the north wherever growth conditions are favourable.

Scorpidium scorpioides (Hedw.) Limpr. Gillam (*C*-7371; *C*-7372; *C*-7478; *S*-1449). In wet sedge meadows, submerged in shallow water or emergent at the edges of pools.

BRACHYTHECIACEAE

Tomenthypnum nitens (Hedw.) Loeske. Gillam (*C*-7362; *C*-7374; *C*-7461; *C*-7482a). In wet sedge meadows, open peat bogs, and also found on a shaded bank in a spruce forest.

Brachythecium salebrosum var. *turgidum* (Hartm.) Lindb. Gillam (*C*-7492). This is very definitely northern in distribution and has been reported from many widely separated places across the continent. Many of the specimens on which such records were based seem doubtfully to belong here, however; and I suspect that it is rather uncommon but distributed pretty much throughout the North.

Eurhynchium pulchellum (Hedw.) Jenn. Sky Pilot Creek (*S*-1113 *p.p.*, with *Saelania glaucescens*); Gillam (*S*-1467; *S*-1483). On soil of protected banks and on soil over rock. Var. *praecox* (Hedw.) Limpr. Gillam (*S*-1457). On bark of roots of a dead, fallen spruce tree.

ENTODONTACEAE

Pleurozium schreberi (Brid.) Mitt. Gillam (*C*-7495). Kettle Rapids (*C*-7560). On dry humus in spruce and white birch stands.

PLAGIOTHECIACEAE

Plagiothecium laetum BSG. A small specimen was collected at Gillam for cytological study (cytological voucher 117, *Crum*). Unfortunately no information on habitat is available. The small size and the erect capsules with the cilia of the endostome lacking or single and very rudimentary seem to leave no doubt of the identification of this species which Grout (1928–40) cited from "New England, New York, Pennsylvania, eastern Canada, and New Mexico." Persson and Weber (1958) recently reported it from Alaska (Mt. McKinley region). It is fairly common at Churchill, Manitoba.

HYPNACEAE

Pylaisia polyantha (Hedw.) BSG. Kettle Rapids (*C*-7544); Gillam (*S*-1457 *p.p.*, with *Eurhynchium pulchellum* var. *praecox; S*-1459). On a shaded rock in a dry spruce–white birch stand at the top of the river-bank, on the bases of small trees and on the bark of roots of a fallen, dead spruce.

Amblystegiella sprucei (Bruch) Loeske. Gillam (*C*-7398; *C*-7434 *p.p.*, with *Distichium capillaceum; C*-7438). On a moist, shaded bank and in a damp, dark hole in the floor of a moist spruce forest; also on the bank of a sedge meadow.

Isopterygium pulchellum (Hedw.) Jaeg. Gillam (*C*-7414; *S*-1483 *p.p.*, with *Eurhynchium pulchellum; S*-1487). Kettle Rapids (*C*-7545). On deeply shaded, damp soil banks and on a shaded, wet rock.

Hypnum bambergeri Schimp. Gillam (*C*-7516). In a wet depression, spruce-larch forest.—Grout (1928–40) knew of collections only from Alberta, British Columbia, the Yukon, and eastern Greenland, as well as two from the Canadian Eastern Arctic (Beechey Island and Wellington Channel). Steere (1948) added three localities on Baffin Island and later reported specimens from Cornwallis Island (1951) and Prince Patrick Island (1955). Kucyniak (1950a) recorded a collection from the Mingan Islands in the Gulf of St. Lawrence. *Hypnum bambergeri* is common at Churchill. Correctly named collections from Southampton Island and the Fosheim Peninsula of Ellesmere Island are also to be found at the National Museum of Canada. Several Alaskan localities are known (Persson, 1954; Sherrard, 1955; Persson & Gjaerevoll, 1957).

Hypnum lindbergii Mitt. Gillam (*C*-7483). Under a spruce tree in a burned-over bog.

Hypnum pratense Hartm. Gillam (*C*-7431). In a moist, shaded depression among sedges and *Sphagnum* in a burned-over bog.

Ptilium crista-castrensis (Hedw.) DeNot. Gillam (*S*-994; *S*-1518). On humus in spruce and spruce-larch woods.

HYLOCOMIACEAE

Hylocomium splendens (Hedw.) BSG. Gillam (C-7436). On humus in dry spruce forests and elsewhere; very common.

RHYTIDIACEAE

Rhytidium rugosum (Hedw.) Kindb. Gillam (*S*-1465). On dry hummock in spruce woods.

POLYTRICHACEAE

Polytrichum commune Hedw. Gillam (*C*-7436). On humus in a dry spruce forest.

Polytrichum gracile Sm. Gillam (*S*-1320). In moist area.

Polytrichum juniperinum Hedw. Gillam (*C*-7409). Kettle Rapids (*C*-7541 *p.p.*, with *Dicranum bergeri*). On dry sand in a jack pine forest and on shaded humus in a dry spruce woods. Var. *alpestre* (Hoppe) BSG. Gillam (*C*-7403; *C*-7456; *C*-7484). In a wet *Eriophorum* bog and also in a rather dry open peat bog.

Polytrichum piliferum Hedw. Gillam (*C*-7459; *C*-7510). On the floor of a dry spruce forest and on sand among jack pines.

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THE SALT MARSH VEGETATION OF CHURCHILL, MANITOBA, AND ITS PHYTOGEOGRAPHIC IMPLICATIONS

Wilfred B. Schofield

Introduction

Much has been written concerning a possible post-Pleistocene marine connection between James Bay and the St. Lawrence River. Potter (1932) originally suggested its existence to explain the presence of the large number of halophytes in James Bay region that were known elsewhere in North America only from the Atlantic seaboard, particularly in the St. Lawrence River estuary.

Opponents to his theory have shown that many of the plants he used to support his conclusions have far wider ranges than he had supposed, and that their presence in James Bay can be explained without recourse to the assumed presence of the marine connection proposed.

Although his critics have diminished the significance of much of Potter's botanical evidence, they have failed to reveal the presence of a larger number of halophytes in the James Bay area than Potter had noted. These plants simply add to the evidence that a post-Pleistocene connection *may* be the best explanation for their presence there.

A large collection of vascular plants made in the vicinity of Churchill, Manitoba, during the summer of 1956 makes it possible to investigate more fully the various theories advanced to explain the distribution of halophytes on Hudson Bay shores.

Only after the information concerning an area has been summarized can one see clearly the gaps that exist in the knowledge. The papers of Ritchie (1956, 1957) provide such a summary for the Churchill region. Scoggan's recent *Flora of Manitoba* (1957) extends the floristic information for the area. The following report will endeavour to supplement these works by reporting native vascular plants of the Churchill region (as defined by Ritchie, 1956) hitherto unknown from Manitoba and those whose range extensions are noteworthy.

The description of vegetation is confined to that of the salt marshes. The floristic affinities of this habitat are discussed, leading to a re-evaluation of the theories of Potter (1932), LaRocque (1949), Boivin (1952), Beecher (1955), and Dutilly, Lepage, and Duman (1958).

Ritchie (1956) describes the various plant communities on the four physiographic formations at Churchill. He subdivides these formations into habitat-types and briefly describes the vegetation of each. In summary, these are:

I. Sand deposits
   - (*a*) sandy foreshore
   - (*b*) open dunes
   - (*c*) stable dunes
   - (*d*) dune slacks
   - (*e*) sandy pools

- II. Outcrop ridge
  - (*a*) heath-type vegetation
  - (*b*) ledges, crevices, and sheltered niches
  - (*c*) lakes, pools, and tarns
  - (*d*) spruce scrub
- III. Plain
  - (*a*) marginal and aquatic vegetation of lakes and pools
  - (*b*) peat bog
  - (*c*) spruce-forest zone
- IV. Gravel ridges
  - (*a*) lichen-heath vegetation of gravel ridge summits
  - (*b*) sedge meadows of poorly drained ridges
  - (*c*) high, large, well-drained ridges inland

Vegetation of the Salt Marshes of Churchill, Manitoba

The salt marsh, which Ritchie does not describe, is located both on the sandy foreshore and on the plain, near the mouth of the Churchill River. In a 1957 paper the same author describes the seres along the Churchill River. It is with part of his "meadow zone" that the following report will be mainly concerned. The "meadow zone," at least in the Churchill area, is more precisely termed a salt marsh inasmuch as the key species in it are predominantly salt marsh species.

This salt marsh reaches its best development in the flats along the Churchill River estuary where it forms a band about one-quarter to one-half mile broad. *Carex subspathacea* is the dominant plant, forming vast green flats. This area is submersed during much of the spring and early summer and accumulates silt, thus building the marsh higher above the floods and ultimately initiating the succession described by Ritchie (1957).

Calamagrostis deschampsioides often forms pure dense "islands" in the *Carex subspathacea* flats, particularly on the drier parts of the marsh, and this grass, with scattered individuals of *Dupontia fisheri* ssp. *psilosantha,* forms a band just below the sere that Ritchie terms the "shrub zone." Occasionally this grassy zone persists farther inland, penetrating among the more elevated patches of shrub zone. Scattered are patches of *Montia lamprosperma, Stellaria humifusa, Triglochin maritima, Chrysanthemum arcticum* ssp. *polaris, Hippuris tetraphylla, Potentilla egedii* var. *groenlandica, Stellaria crassifolia,* and, more rarely, *Cochlearia officinalis* ssp. *groenlandica, Ranunculus cymbalaria, Carex glareosa* var. *amphigena, Puccinellia phryganodes,* and *P. vaginata.* In small pools and trickles that cut through the marsh, *Hippuris tetraphylla* and *Potamogeton filiformis* var. *borealis* are abundant.

In the shrub zone, there are often a number of small mud flats. On the west side of Churchill River these flats are very extensive. They are highly alkaline and saline, frequently possess a thin white crust of salts, and are nearly barren. In several, where conditions are not so extreme, the following vegetation is found:

Triglochin maritima (d)[1]
Pedicularis sudetica (f)
Scirpus rufus var. *neogaeus* (f)
Juncus alpinus var. *rariflorus* (f)

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[1] The symbols used to indicate frequency of species within the community are as follows: (d) dominant, (f) frequent or scattered throughout the community, (o) occasional in the community, (la) locally abundant in favourable habitats, and (r) rarely occurring, represented by very few plants.

Carex microglochin (f)
C. subspathacea (o)
Calamagrostis deschampsioides(o)
Carex saxatilis var. *miliaris* (o)
Eriophorum angustifolium (o)
Carex maritima (la)
Eleocharis pauciflora var. *fernaldii* (la)
Equisetum variegatum (o)
Juncus castaneus (o)
J. albescens (o)
Trichophorum austriacum (o)
Kobresia simpliciuscula (o-r)

In more open dry flats, where salinity and alkalinity are more extreme, the vegetation consists of a marginal band of *Plantago maritima* ssp. *juncoides, Scirpus rufus* var. *neogaeus, Ranunculus cymbalaria,* and *Potentilla egedii* var. *groenlandica.* Scattered over the flats are colonies of *Suaeda ?maritima, Salicornia europaea,* and clumps of *Puccinellia lucida* or *P. nuttalliana.* Very rarely *Carex ursina* and *Lomatogonium rotatum* are found in such flats.

Unfortunately no detailed descriptions of salt marshes along the coast of Hudson Bay were made in the field. These marshes are frequently very similar to those of the Churchill River estuary but possess a sandier soil and a consequent local distribution of such species as *Polygonum boreale, Koenigia islandica, Montia lamprosperma, Catabrosa aquatica, Stellaria crassifolia, Atriplex patula, A. glabriuscula, Spergularia marina, Galium trifidum* var. *halophilum, Hutchinsia procumbens, Juncus bufonius* var. *halophilus,* etc. On the upper margins of the marsh, the grasses *Hordeum jubatum* and *Calamagrostis neglecta* are often very important. *Puccinellia langeana* occasionally forms tufted masses at upper tide level along some parts of the coast near Churchill. Along the margins of a streamlet through one marsh, *Arctophila fulva* was the dominant grass, and *Ranunculus hyperboreus* was abundant in the water.

Analysis of the Affinities of the Maritime Vascular Flora of the James Bay Region

The large number of obligate halophytes known from the James Bay region reveals that (1) the area has been more thoroughly explored than almost any other part of coastal Hudson Bay and (2) the available habitats for such halophytes are relatively extensive.

The obligate halophytes of James Bay may be divided into six phytogeographic groups, based on the region of greatest affinity. The lists below have been compiled from the papers of Dutilly, Lepage, and Duman (1954, 1958).

1. Arctic — confined largely to the Arctic Archipelago but reaching occasionally into the subarctic (*see* map 1).

Puccinellia andersonii (Porsild, 1957, map 47)
P. phryganodes (Porsild, 1957, map 50)
P. vaginata (Porsild, 1957, map 52)
Carex subspathacea (Porsild, 1957, map 87)
Matricaria ambigua (Porsild, 1957, map 315)

2. Eastern American — found mainly in eastern North America but extending as far west as the west coast of Hudson Bay and occasionally farther (*see* maps 2 and 3).

Poa eminens
P. labradorica (Dutilly, Lepage & Duman, 1958, fig. 5)
Puccinellia laurentiana
P. macra (Dutilly, Lepage & Duman, 1954, fig. 4)
Carex paleacea (Potter, 1932, map 5)
C. salina var. *kattegatensis*
Eleocharis halophila
Scirpus paludosus var. *atlanticus*
Juncus balticus var. *stenocarpus* (Dutilly, Lepage & Duman, 1954, fig. 8)
Polygonum fowleri (Fernald, 1925, map 25)
Atriplex glabriuscula
A. patula var. *littoralis*
Salicornia europaea var. *prostrata*
S. europaea var. *simplex*
Suaeda americana
Cochlearia officinalis ssp. *groenlandica*
Ligusticum scothicum (Rouleau, 1950, fig. 6)
Euphrasia arctica (Porsild, 1957, map 289)

3. Western American — occurring mainly west of Hudson Bay and only occasionally reaching the east coast of the bay (*see* map 4).

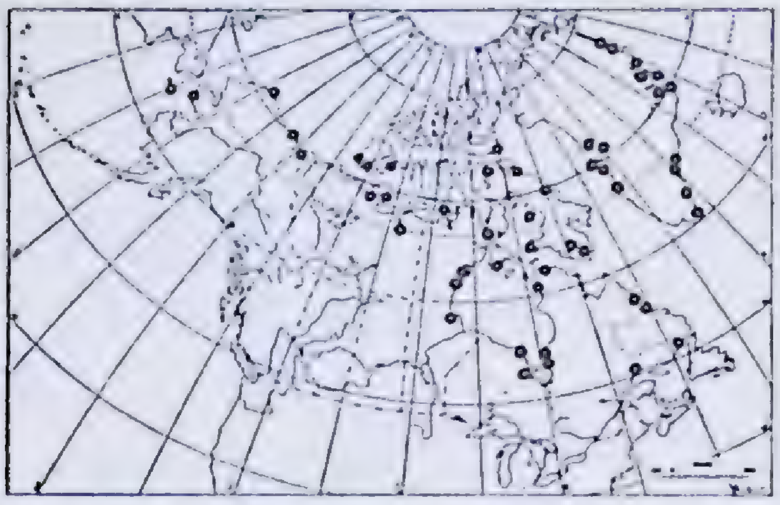
Calamagrostis deschampsioides
Cochlearia officinalis ssp. *arctica*

4. Eastern-Western American Disjuncts — found in eastern North America and in far western or northwestern North America, but with few or no localities known between. These may later be proved to be better grouped with the Western American group as the Northwest becomes better explored botanically (*see* map 5).

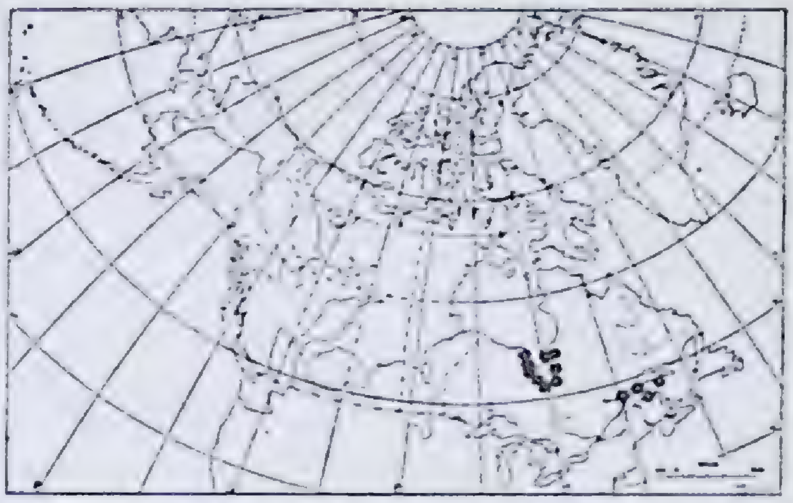
Puccinellia langeana
P. lucida
P. pumila
Eleocharis kamtschatica
Carex salina
Polygonum boreale
Spergularia canadensis (Rossbach, 1940, map 6)
Coelopleurum lucidum
Chrysanthemum arcticum ssp. *polaris*

5. Widespread Boreal and Subarctic (*see* map 6).

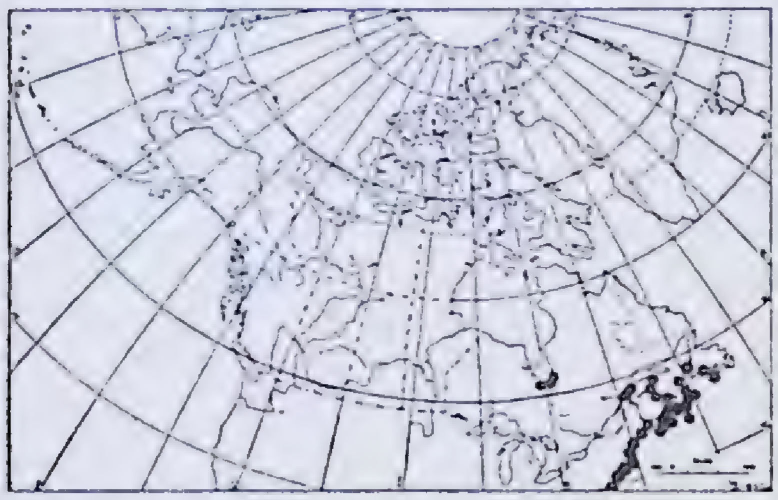
Zannichellia palustris var. *major* (Potter, 1932, map 2)
Zostera marina var. *stenophylla* (Potter, 1932, map 10)
Carex glareosa var. *amphigena* (Porsild, 1957, map 82)
C. mackenziei (Potter, 1932, map 1)
Honkenya peploides (Porsild, 1957, map 146)
Stellaria humifusa (Porsild, 1957, map 136)
Potentilla egedii var. *groenlandica* (Porsild, 1957, map 226)
Lathyrus japonicus var. *japonicus*
L. japonicus var. *aleuticus*
Hippuris tetraphylla
Mertensia maritima (Porsild, 1957, map 284)



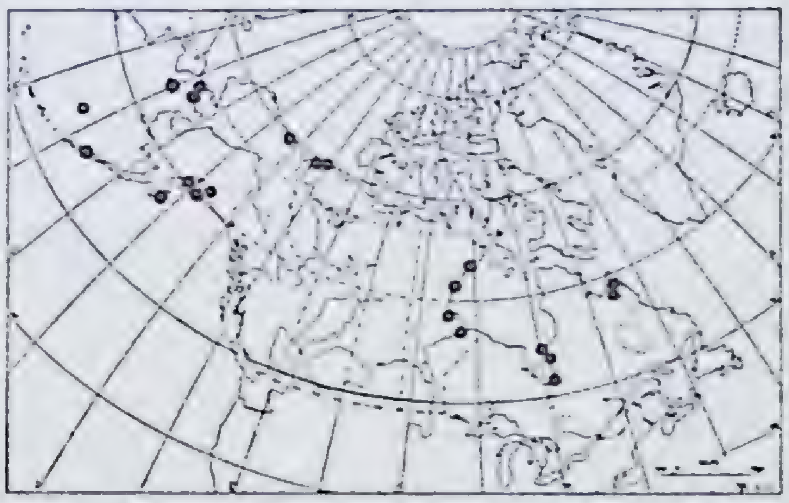
MAP. 1. Arctic group: American range of *Carex subspathacea* (from Porsild, 1957, map 87).



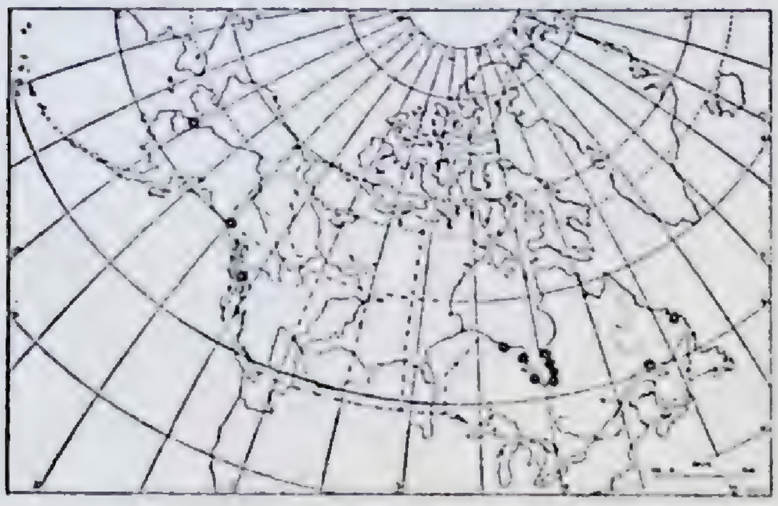
MAP 2. Eastern American group: American range of *Juncus balticus* var. *stenocarpus* (from Dutilly, Lepage & Duman, 1954, fig. 8).



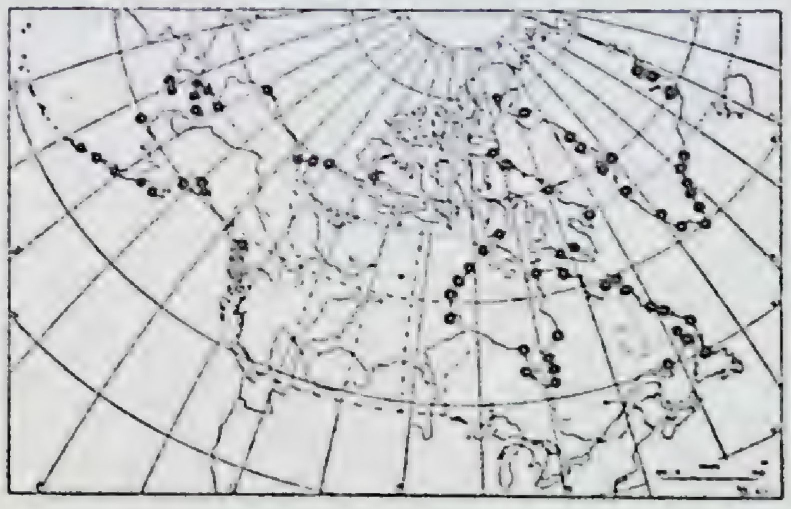
MAP 3. Eastern American group: American range of *Eleocharis halophila*.



MAP 4. Western American group: American range of *Calamagrostis deschampsioides*.



MAP 5. Eastern-Western American disjunct group: American range of *Eleocharis kamtschatica* (from Hultén, 1941-1950, map 214, and Dutilly, Lepage & Duman, 1958, fig. 8).



MAP 6. Widespread Boreal and Subarctic group: American range of *Carex glareosa* var. *amphigena* (from Porsild, 1957, map 82).

6. Widespread Maritime — some also occasionally found inland, especially in saline or alkaline habitats (*see* map 7).

Catabrosa aquatica
Dupontia fisheri ssp. *psilosantha* (Porsild, 1957, map 44)
Elymus arenarius ssp. *mollis* (Porsild, 1957, map 57)
Scirpus rufus var. *neogaeus*
Juncus bufonius var. *halophilus*
Atriplex patula
Salicornia europaea
Spergularia marina (Rossbach, 1940, maps 7 and 8)
Glaux maritima var. *obtusifolia* (Potter, 1932, map 4)
Plantago maritima ssp. *juncoides* (Potter, 1932, map 8)[1]

Dutilly, Lepage, and Duman (1954, 1958) have also noted a large number of hybrid species of *Carex* (such as *C. exsalina*, *C. flavicans*, *C. gardneri*, and *C. dumanii*) which, if their parentage has any influence on their habitat specificity (as it seems), would be confined to the salt marsh or to its upper margins. These hybrids are apparently present at their place of origin.

From the above lists it may be noted that the bulk of the halophytes of the James Bay region are Eastern American or Widespread American species, a high proportion of them unknown from the Labrador Peninsula (*see* Table I).

ANALYSIS OF THE AFFINITIES OF THE MARITIME VASCULAR FLORA OF CHURCHILL

The obligate halophytes of Churchill fall into seven phytogeographic groups, six of which are also represented in the maritime flora of James Bay:

1. Arctic

Puccinellia phryganodes
P. vaginata
Carex ursina (Porsild, 1957, map 77)
C. subspathacea
Matricaria ambigua

2. Eastern American

Puccinellia vaginata var. *paradoxa* (Porsild, 1957, map 52)
Suaeda maritima
Atriplex glabriuscula
Cochlearia officinalis ssp. *groenlandica*
Galium trifidum var. *halophilum*

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[1] The distributions of the above species, as well as all others considered in this report, were gleaned from the publications of Abbe (1936, 1955), Dutilly, Lepage, and Duman (1948, 1951, 1953, 1954, 1958), Fernald (1925, 1950), Gardner (1937, 1946), Hultén (1941-1950), Hustich (1957, 1957a), Marie-Victorin (1948), Porsild (1951, 1955, 1957), Raup (1943, 1947), Raymond (1950), Rouleau (1956), and Scoggan (1957).

3. Western American
    - *Calamagrostis deschampsioides*

4. Eastern-Western American Disjuncts
    - *Puccinellia langeana*
    - *P. lucida*
    - *Chrysanthemum arcticum* ssp. *polaris*
    - *Polygonum boreale*

5. Widespread Boreal and Subarctic
    - *Zostera marina* var. *stenophylla*
    - *Puccinellia deschampsioides*
    - *Carex glareosa* var. *amphigena*
    - *C. mackenziei*
    - *Honkenya peploides*
    - *Stellaria humifusa*
    - *Potentilla egedii* var. *groenlandica*
    - *Hippuris tetraphylla*
    - *Mertensia maritima*

6. Widespread Maritime
    - *Elymus arenarius* ssp. *mollis*
    - *Dupontia fisheri* ssp. *psilosantha*
    - *Carex maritima*
    - *Scirpus rufus* var. *neogaeus*
    - *Salicornia europaea*
    - *Spergularia marina*
    - *Lathyrus japonicus* var. *aleuticus*
    - *Plantago maritima* ssp. *juncoides*
    - *Matricaria ambigua*

7. Maritime Ecotypes — Some plants behave as littoral or halophytic species over much of their range, especially in eastern North America, but are otherwise found inland mainly in mountainous areas. These are presumably different ecotypes. In the area concerned, at least, these species probably extend their range mainly via the sea-coast (*see* map 8). They are represented in Churchill by the following:

    - *Montia lamprosperma*
    - *Alopecurus alpinus*
    - *Koenigia islandica*
    - *Ranunculus pallasii*
    - *Hutchinsia procumbens*

Many other species termed "indifferent halophytes" by Svenson (1927) and Potter (1932) probably also extend their area in much of eastern North America largely via the sea-coast. These are well represented at Churchill. The following belong in this category: *Juncus bufonius* var. *halophilus, J. balticus* var. *littoralis, Catabrosa aquatica, Hordeum jubatum, Hierochloë odorata*, and *Lomatogonium rotatum*.

TABLE I—DISTRIBUTION OF MARITIME VASCULAR PLANTS OF HUDSON BAY

Key: The phytogeographic groupings coincide mainly with those given earlier. a—Arctic e—Eastern American w—Western American x—Widespread Boreal and Subarctic	Pacific Coastal Alaska	Arctic Coastal Alaska	Arctic Coastal Mackenzie District	Boothia Peninsula	Canadian Western Arctic Archipelago	Churchill, Manitoba	James Bay Region	Richmond Gulf, Quebec	Northernmost Quebec	Ungava Bay, Quebec	Northernmost Labrador	Canadian Eastern Arctic Archipelago	Hamilton Inlet and Melville Peninsula	Gulf of St. Lawrence	Inland west of James Bay
Zostera marina var. *stenophylla*	x					x	x						x	x	
Zannichellia palustris var. *major*	x						x							x	
Ruppia maritima s.l.							e						e	e	
Calamagrostis deschampsioides	w		w			w	w				w				
Catabrosa aquatica						x	x	x						x	x
Dupontia fisheri ssp. *psilosantha*	x	x	x		x	x	x	x		x	x	x	x		x
Elymus arenarius ssp. *mollis*	x	x	x	x	x	x	x		x		x	x	x	x	x
Poa eminens	e						e	e			e		e	e	
P. labradorica							e	e							
Puccinellia andersonii		a			a		a					a			
P. deschampsioides						x									
P. langeana	x	x				x	x								
P. laurentiana							e								e
P. lucida						x	x								x
P. macra							e								e
P. phryganodes	a		a	a	a	a	a		a	a	a	a	a		
P. pumila	x		x				x							x	
P. vaginata			a		a	a	a					a			
P. vaginata var. *paradoxa*						e						e			
Eleocharis halophila							e							e	
E. kamtschatica	w						w							w	
Scirpus rufus var. *neogaeus*	x					x	x							x	
S. paludosus var. *atlanticus*							e							e	
Carex glareosa var. *amphigena*	x		x		x	x	x	x	x	x	x	x	x	x	
C. mackenziei	x					x	x							x	
C. maritima	x	x	x		x	x	x	x	x	x		x	x	x	x
C. paleacea							e	e					e	e	
C. salina var. *salina*							e							e	
C. salina var. *kattegatensis*							e	e					e	e	
C. subspathacea	a	a	a		a	a	a		a		a	a		a	
C. ursina		a	a		a	a	a		a			a			
Juncus balticus var. *stenocarpus*							e							e	
J. bufonius var. *halophilus*						x	x							x	
Koenigia islandica	x		x			x	x		x		x	x			x
Rumex maritimus var. *fueginus*	x					x	x							x	
Polygonum fowleri							e							e	
P. boreale	x					x	x							x	

TABLE I—DISTRIBUTION OF MARITIME VASCULAR PLANTS OF HUDSON BAY—(*Cont'd.*)

Key: The phytogeographic groupings coincide mainly with those given earlier. a—Arctic e—Eastern American w—Western American x—Widespread Boreal and Subarctic	Pacific Coastal Alaska	Arctic Coastal Alaska	Arctic Coastal Mackenzie District	Boothia Peninsula	Canadian Western Arctic Archipelago	Churchill, Manitoba	James Bay Region	Richmond Gulf, Quebec	Northernmost Quebec	Ungava Bay, Quebec	Northernmost Labrador	Canadian Eastern Arctic Archipelago	Hamilton Inlet and Melville Peninsula	Gulf of St. Lawrence	Inland west of James Bay
Atriplex patula	...	...	...	...	...	e	e	...	...	...	...	...	...	e	...
A. patula var. *littoralis*	...	...	...	...	...	...	e	...	...	...	...	...	...	e	...
A. glabriuscula	...	...	...	...	...	e	e	...	...	...	...	...	...	e	...
Salicornia europaea	...	...	...	...	...	e	e	...	...	...	...	...	...	e	...
S. europaea var. *simplex*	...	...	...	...	...	...	e	...	...	...	...	...	...	e	...
S. europaea var. *prostrata*	...	...	...	...	...	...	e	...	...	...	...	...	...	e	...
Suaeda americana	...	...	...	...	...	...	e	...	...	...	...	...	...	e	...
S. maritima	e	...	...	...	...	e	...	...	...	...	...	...	...	e	...
Montia lamprosperma	x	...	x	...	x	x	x	x	x	...	x	x	x	x	...
Spergularia canadensis	...	...	...	...	...	...	x	...	...	...	...	...	...	x	...
S. marina	...	...	...	...	...	x	x	...	...	...	...	...	...	x	...
Honkenya peploides	x	x	x	...	x	x	x	...	x	x	x	x	x	x	...
Stellaria humifusa	x	x	x	x	x	x	x	...	x	x	x	x	x	x	...
Ranunculus hyperboreus	x	x	x	x	x	x	x	...	x	x	x	x	x	x	x
R. pallasii	w	w	w	...	...	w	w	...	w	...	w	w	...	...	w
R. cymbalaria	x	...	...	...	x	x	x	...	...	...	...	...	x	x	x
Hutchinsia procumbens	...	...	...	...	...	x	...	...	...	...	...	...	...	...	x
Cochlearia officinalis ssp. *arctica*	w	w	w	...	w	...	w	...	...	...	...	...	w	...	...
C. officinalis ssp. *groenlandica*	...	...	...	e	...	e	e	e	e	e	e	e	e	...	...
Potentilla egedii var. *groenlandica*	x	...	x	...	x	x	x	...	x	x	x	x	...	x	...
P. pulchella	a	a	a	a	a	a	a	a	a	...	...	a	...	...	...
Lathyrus japonicus var. *aleuticus*	x	...	...	...	...	x	x	...	...	...	...	...	x	x	...
L. japonicus var. *glaber*	...	...	...	...	...	x	x	x	...	...	...	...	x	x	...
Hippuris tetraphylla	x	x	...	...	...	x	x	...	...	...	...	...	x	...	...
Ligusticum scothicum	...	...	...	...	...	...	e	e	...	...	...	...	e	e	...
Coelopleurum lucidum	x	...	...	...	...	...	x	...	...	...	...	...	x	x	...
Glaux maritima var. *obtusifolia*	x	...	...	...	...	...	x	...	...	...	...	...	...	x	...
Lomatogonium rotatum	x	...	x	...	x	x	x	...	...	x	...	...	x	x	x
Mertensia maritima	x	x	x	x	x	x	x	x	x	x	x	x	x	x	...
Euphrasia arctica	...	...	e	...	...	e	e	...	e	e	e	e	e	e	e
Plantago maritima ssp. *juncoides*	x	...	...	...	...	x	x	x	...	x	x	x	x	x	x
Galium trifidum var. *halophilum*	...	...	...	...	...	e	...	...	...	...	...	...	...	e	...
Matricaria ambigua	a	a	a	a	a	a	a	...	a	a	a	...	...	...	a
Chrysanthemum arcticum ssp. *polaris*	x	x	x	...	...	x	x	x	x	...	...	...	...	...	...

Analysis of the Affinities of the Non-maritime Vascular Flora of Churchill

The entire vascular flora of Churchill may be assigned the same phytogeographic divisions as the above. The lists below exclude the halophytes already mentioned.

1. Arctic—Porsild, 1957, gives maps of the ranges of the following plants:

Poa arctica ssp. *caespitans*
Dupontia fisheri var. *aristata*
Arctophila fulva
Arctagrostis latifolia
Hierochloë pauciflora
Carex amblyorhyncha
C. atrofusca
C. misandra
C. stans
C. membranacea
Luzula confusa
Cerastium alpinum
C. alpinum var. *glanduliferum*
Melandrium apetalum ssp. *arcticum*
M. affine
Draba alpina
D. cinerea
Lesquerella arctica
Eutrema edwardsii
Potentilla nivea ssp. *chamissonis*
P. pulchella

2. Arctic-alpine—whose range extends southward beyond arctic regions via high altitudes and exposed arctic-like habitats. Most of the plants listed below have their ranges mapped in Porsild, 1957.

Lycopodium selago var. *adpressum*
Trisetum spicatum var. *maidenii*
Kobresia myosuroides
Carex rupestris
C. bicolor
C. capillaris
C. microglochin
Juncus biglumis
J. albescens
J. castaneus
Bistorta vivipara
Minuartia rossii
Arenaria humifusa
Draba lactea
D. lanceolata
Saxifraga aizoides
S. oppositifolia
S. rivularis
Hedysarum mackenzii
Chamaenerion latifolium
Loiseleuria procumbens
Rhododendron lapponicum
Campanula uniflora
Erigeron humilis
Arnica alpina ssp. *attenuata*

3. Eastern American

Festuca prolifera (Fernald, 1933, map 14)
Eriophorum vaginatum ssp. *spissum*
Carex norvegica (Porsild, 1957, map 88)
C. bigelowii (Porsild, 1957, map 84)
C. saxatilis var. *miliaris* (Porsild, 1957, map 99)
C. saxatilis var. *rhomalea* (Porsild, 1957, map 100)
Juncus arcticus (Porsild, 1957, map 103)
Salix cordifolia var. *callicarpaea* (Porsild, 1957, map 122)
S. cordifolia var. *tonsa*
S. calcicola (Porsild, 1957, map 116)

S. anglorum
S. cordata
Betula minor
Draba minganensis
Arabis alpina (Porsild, 1957, map 196)
A. arenicola var. *pubescens* (Porsild, 1957, map 197)
Saxifraga caespitosa ssp. *eucaespitosa* (Porsild, 1957, map 208)
S. caespitosa ssp. *exaratoides* (Porsild, 1957, map 210)
Oxytropis campestris var. *johannensis* (Barneby, 1952, map 8)
O. terrae-novae (Porsild, 1957, map 250)
Euphrasia arctica (Porsild, 1957, map 289)
Bartsia alpina (Porsild, 1957, map 290)
Pedicularis flammea (Porsild, 1957, map 294)

4. Western American
Bromus pumpellianus
Carex rotundata
C. physocarpa (Raup, 1947, plate XIX)
Cypripedium passerinum (Raup, 1947, plate XX)
Salix glauca var. *acutifolia* (Raup, 1947, plate XXI)
S. alaxensis (Porsild, 1957, map 120)
S. alaxensis var. *obovalifolia*
S. arbusculoides (Raup, 1947, plate XXII)
S. brachycarpa var. *antimima*
S. brachycarpa var. *mexiae*
Monolepis nuttalliana
Descurainia sophioides (Porsild, 1957, map 179)
Draba luteola
Ribes oxyacanthoides
R. hudsonianum (Raup, 1947, plate XXVII)
Fragaria glauca (Raup, 1947, plate XXVIII)
Geum macrophyllum var. *perincisum* (Raup, 1947, plate XXIX)
Oxytropis campestris var. *varians*
Linum lewisii (Porsild, 1957, map 254)
Cicuta mackenzieana
Gentiana affinis
Castilleja raupii
Pedicularis sudetica (Porsild, 1957, map 298)
Erigeron acris var. *elatus* (Raup, 1947, plate XXXV)
E. lonchophyllus
Artemisia tilesii var. *elatior* (Porsild, 1957, map 320)
Antennaria rosea (Porsild, 1950, map 30)

5. Eastern-Western American Disjuncts
Gentianella propinqua (Raup, 1947, plate XXXIII)
Anemone richardsonii (Porsild, 1957, map 160)
Draba aurea
Carex williamsii

6. Widespread Boreal and Subarctic — This group constitutes the great bulk (71%) of the flora, being all species not occurring in the above lists.

The table given below shows clearly the structure of the flora of Churchill. The "Boreal and Arctic Widespread" grouping is admittedly artificial and could be readily broken into several groups. For convenience alone, the "Maritime Ecotypes" have been included in this group.

TABLE II.—A SUMMARY OF THE AFFINITIES OF THE NATIVE VASCULAR FLORA OF CHURCHILL

Phytogeographic Type	Total Maritime Flora (38 species)		Total Flora (incl. maritime) (397 species)	
	No. of species	Approx. % of Total species	No. of species	Approx. % of Total species
Arctic	5	13	26	6.5
Arctic-alpine	—	—	26	6.5
Eastern American	5	13	28	7
Western American	1	3	28	7
East-West American Disjunct	4	11	8	2
Boreal and Subarctic Widespread	23	60	281	71

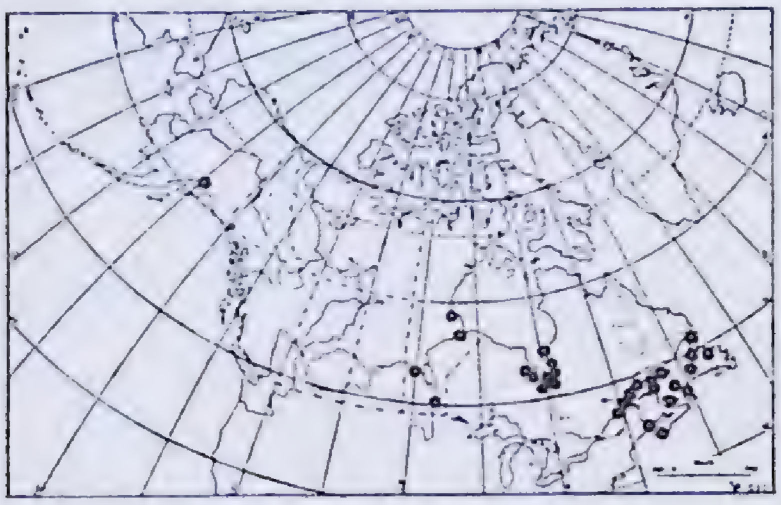
Dutilly, Lepage, and Duman (1954) note that in the James Bay region "la plupart des plantes arctiques et subarctiques... se rencontrent le long de la côte seulement." Such is certainly the case at Churchill, since the available arctic-type habitats are present on the exposed headlands of the outcrop ridge and in the boggy windswept flooded lowlands behind them. Inland the spruce forest has encroached upon the terrain, and the bulk of suitable niches for arctic and subarctic species has been destroyed.

HYPOTHESES TO EXPLAIN DISTRIBUTION OF MARITIME PHANEROGAMS ON HUDSON BAY SHORES

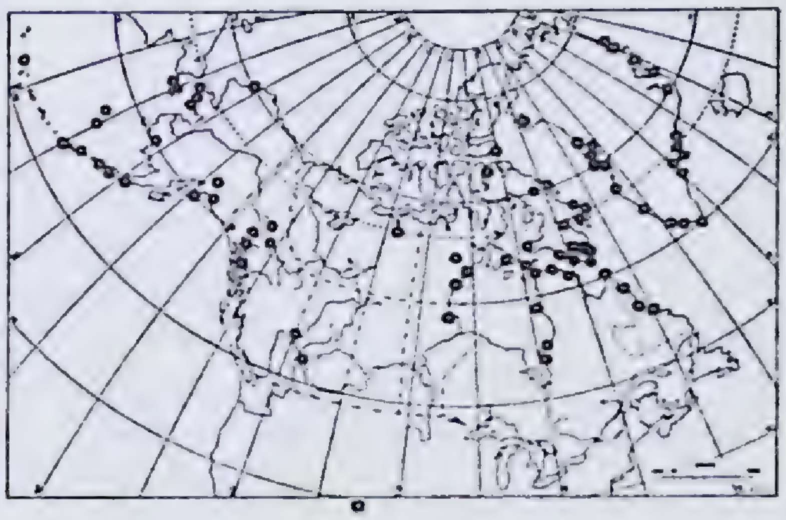
The presence of obligate halophytes in James Bay, otherwise known in North America only "along the Atlantic seaboard, about the region of the Gulf of St. Lawrence," led Potter (1932) to postulate a post-Pleistocene marine connection between Hudson Bay and the St. Lawrence. As shown by Porsild (1932), Polunin (1940), LaRocque (1949), and Boivin (1952), many of the plants used by Potter possess a far wider distribution around the coast of the Labrador Peninsula and Hudson Bay than Potter had realized.

In recent years, particularly because of extensive collections made by Dutilly, Lepage, and Duman, the list of obligate halophytes known from James Bay area has increased conspicuously (summarized in Dutilly, Lepage & Duman, 1954, 1958). Then, too, exploration by the same persons (1948, 1951, 1953, 1958), as well as by Gardner (1937, 1946), Rouleau

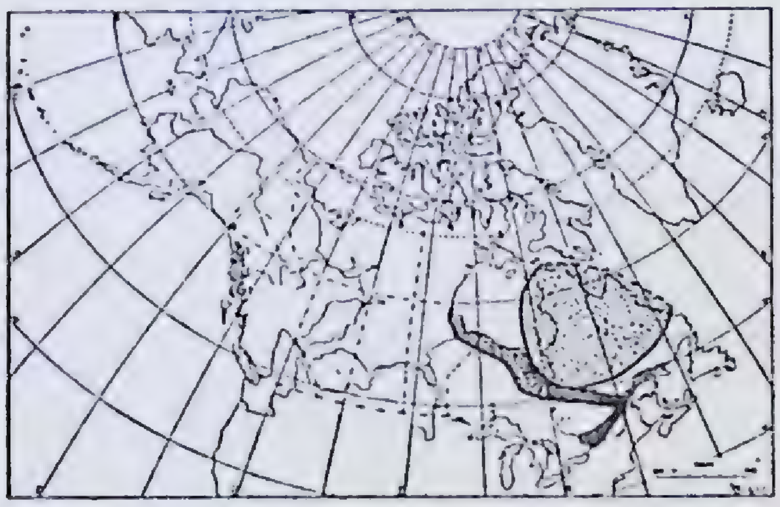
(1956) and others, shows that the ranges of many of the species extend around the Labrador Peninsula and thence to Hudson Bay. Much exploration remains to be done, for the salt-marsh areas are often extremely difficult to botanize and are accessible only from the sea in much of the area concerned. Even at Churchill, where numerous botanists have collected, the salt marsh habitat has been badly neglected. This is probably also the case for more briefly visited areas around Hudson Bay.



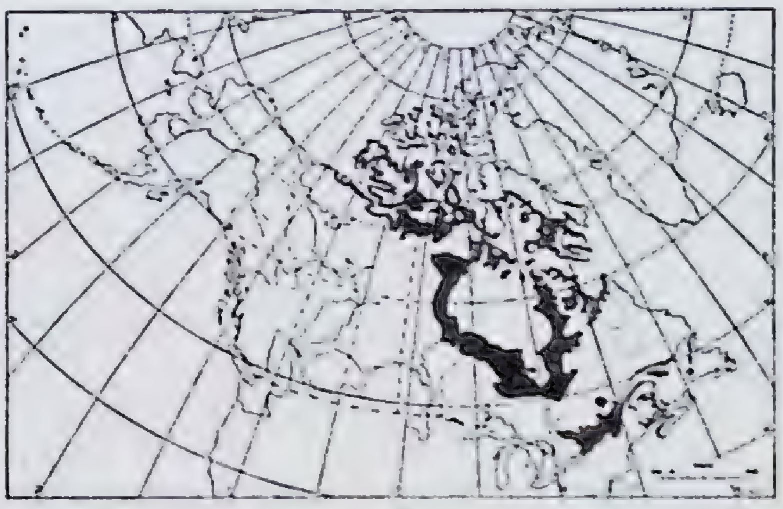
Map 7. Widespread maritime group: American range of *Scirpus rufus* var. *neogaeus*.



Map 8. Maritime ecotype group: American range of *Koenigia islandica* (from Porsild, 1957, map 128).



Map 9. Possible post-Pleistocene marine connection between James Bay and the Gulf of St. Lawrence (from LaRocque, 1949). Stippled area represents ice; the horizontal-lined area represents the marine connection.



Map 10. Post-Pleistocene marine submergence in northern North America (exclusive of the United States). (From Geological Association of Canada, Glacial Map of Canada, 1958).

LaRocque (1949) demonstrates that the location of the migration route proposed by Potter is improbable on geological and palæontological grounds and suggests an alternative route that is more reasonable on the same grounds (*see* map 9.) The recent glacial map of Canada, compiled by the Geological Association of Canada (1958), shows Lake St. John, Quebec, with postglacial marine sediments 575 feet above the present sea-level (*see* map 10). These sediments are shown to surround the lake, but information was apparently inadequate to show where this joined the sea. LaRocque suggests that it might have connected James Bay and the St. Lawrence River, but he notes the lack of palæontological exploration of this area and a consequent absence of proof or refutation of the route.

Boivin (1952) explains the distribution of the halophytic species in James Bay by pointing out that many of the species used by Potter (1932) to support his theory show a distribution that indicates a wide habitat tolerance, and the remainder of strict halic tolerance could have "reached the James Bay region by following the outer sea coast around the Labrador Peninsula." This latter statement he supports by demonstrating that many of the halophytes concerned are known to have a fairly general distribution (with some gaps) around the Labrador Peninsula.

He gives an alternative theory, stated as follows: "They could have first reached the upper Ottawa region via the Champlain sea coast. They could then have colonized the coast and shores of the glacial lake a few miles away to the north. As the shoreline was displaced gradually to the north, first with the successively lower levels of the glacial lake, then with the progressively lower Hudson Bay waters, these plants were presumably able to colonize each successive shoreline until they reached their present location."

Dutilly, Lepage, and Duman (1958) explain the presence of the halophytes and other plants of eastern affinities in James Bay by noting that during the "xerothermic" interval (presumably anathermal plus hypsothermal intervals, *see* Cooper, 1958) after the disappearance of the Labrador glacier, there was a considerable northward migration of species suited to this warmer climate. They draw attention to the fact that a shorter coastline of the Labrador Peninsula, owing to marine submergence, would give the halophytes a shorter distance to go around the Peninsula and to Hudson Bay and ultimately to James Bay (*see* map X). With cooling of climate, the plants have persisted in areas where conditions still favour it. These authors note also that owing to the successive glacial advances many species were conspicuously reduced in biotypes. Thus some species were not equipped genetically to extend their range far from the southern margin of the glacial boundary where they survived the glaciations.

Beecher (1955) suggests that if there were not a complete connection of James Bay and the St. Lawrence River during post-Pleistocene time, the distance from one body of water to the other would have been relatively short, and halophytes might have reached James Bay via this route.

Discussion and Conclusions

As is clearly shown by the lists of maritime species of the James Bay region given above, there is a remarkably large number of obligate halophytes or species that tend to extend their range via the sea-coast. It is unreasonable to assume that the majority of these species had any different ecological requirements when they were invading territory newly exposed by receding glaciers than they have now. The present ecological behaviour of several species in the west, represented by "maritime ecotypes" in the east, suggests that the populations in the east were previously not so restricted by habitat. The maritime ecotypes survived because of the availability of the suitable ecological niche, and the non-maritime ecotypes were eliminated owing to its absence at that time. In consequence these species extended their ranges in eastern America via sea shores.

It may be argued that some presumed obligate maritime species are now found around fresh-water lakes far from the sea. In the vast majority of cases, as in that of *Ammophila breviligulata* and *Lathyrus japonicus* at Lake St. John, Quebec (*see* Raymond, 1950), the species of general maritime distribution reached the lake by following a sea-coast that has since disappeared. They persist only because they possess sufficient ecological amplitude, and may have evolved a non-maritime race by isolation from the widespread maritime population. This is further evidence that although some plants of maritime distribution have been able to survive in non-maritime situations, they have extended their ranges by following sea-coasts. It seems probable, therefore, that the maritime species of eastern affinities reached James Bay via sea shores and not by lake shores as Boivin (1952) suggests.

The absence of unglaciated areas in the Hudson Bay region or in Quebec-Labrador Peninsula has been amply demonstrated both on geological (Geological Association of Canada, 1958) and botanical (Rousseau, 1953) grounds. The possibility of a refuge within this region can be excluded as a source for the plants of the area under discussion.

As shown by Table II, the affinities of the total vascular flora of Churchill are in very different proportions to those of the maritime vascular flora alone. The ratio of Eastern American maritime (13%) and Western American maritime (3%) species is particularly notable. This cannot be explained on the basis of proximity to the areas where the species survived glaciation, for even when post-Pleistocene submergence is taken into account, the distance from these areas on either side of the continent (northwest or southeast) was nearly the same, unless one agrees with the basic hypothesis of Potter. In the latter case the distance from the eastern American refuge would have been conspicuously shorter.

It is not surprising that the total number of non-maritime Western species in the region is higher than that of species from the east. The refuges for the western plants were twofold: in the unglaciated area of Alaska and Yukon, and south of the glacial boundary (in the United States). There are elements from the northwest (*Salix alaxensis*, *Castilleja raupii*, and *Pedicularis sudetica* among them) showing clearly that this route was apparently open for migration from the north before it was colonized and closed by the flora that encroached from the south.

As the lists show, most of the western species of the region are widely distributed in western North America. The inland vegetation, however, would have no effect on the extension of the range of species via the sea-coast.

Porsild (1955) states that the strand flora of the Canadian Western Arctic Archipelago is very small. This he attributes to ice-shove. This would have been even more extreme during the early post-Pleistocene. The effect of this upon the composition of the flora eastward is readily noted by reference to Table I. Only two species of specifically Western Maritime range (*Cochlearia officinalis* ssp. *arctica* and *Calamagrostis deschampsioides*) are represented. Probably the disjuncts *Eleocharis* *kamtschatica* and *Ranunculus pallasii* could be included in this category as well. During early post-Pleistocene time, as now, there must have been considerable sea-ice. This presumably caused considerable ice-shove and made the coast of the Quebec-Labrador Peninsula an extremely poor migration route for maritime plants. The Labrador coast, in particular, possesses very few suitable strand habitats, because it is a drowned coast.

After the great masses of sea-ice had disappeared and the anathermal period had produced conditions favourable for northward migration of the vegetation, the coast was still poor in strand habitats, so that although climatic conditions were suitable for more maritime species to extend their ranges far north of their present range, there is no good reason to assume that they did so.

There is presently no evidence to suggest that there was an extended coastal plain along the Labrador coast during glacial or post-glacial time which would have served as a suitable migration route for the species under discussion. Indeed greater submergence can be inferred because of the depression of the land by the ice-sheet. Recovery from this depression has yielded very little land on the Labrador coast (*see* map of Geological Association of Canada, 1958).

Why, then, is there a large number of maritime vascular plants from eastern sources? It might be suggested that Eastern American maritime plants are more aggressive, thus excluding through competition any western colonists that had established themselves earlier. So far there is no evidence to support this.

Could the maritime plants have "jumped" the gap between the Champlain Sea and the submerged Hudson Bay Lowland? Potter (1932) discusses this in some detail and concludes that it is highly improbable. He discards the possible importance of wind, birds, and other animals on the basis of rather little evidence. As Turrill (1951) states, "...there is very little reliable evidence for or against long-distance transport, other than by ocean currents and by man."

Potter (1932) gives convincing evidence that ocean currents were probably not important in distributing the species around the Quebec-Labrador Peninsula to James Bay. "Had seeds been carried short distances along the coast by this agency and in favorable spots established themselves, and had their progeny been transported in the same manner a short distance farther north, there establishing themselves and so on until the goal had been reached, it would be expected that more traces of the parent stock would be found along the outer coast of Labrador" (loc. cit., p. 82). He notes also that since the Labrador current flows southward along the coast, "it is difficult to understand how water flowing south could be of assistance in the dispersal of seeds towards the north."

Reference to Table I shows the fairly large number of maritime vascular plants found in James Bay and the Gulf of St. Lawrence, and in many cases (twenty) with few or no localities known along the coast of the Quebec-Labrador Peninsula. In the areas northward on the Hudson Bay coast, the species could well have extended northward from the James Bay region.

Since ocean currents can be eliminated on the one hand and the availability of habitats on the other, it is probable that the coast around the Quebec-Labrador Peninsula did not serve as an effective post-Pleistocene migration route for maritime plants to enter the Hudson Bay region. That it may have served as a route later than immediately post-Pleistocene times is likely, and the plants still exist in the areas that they originally colonized.

It is concluded that a post-Pleistocene marine connection between James Bay and the Gulf of Saint Lawrence best explains the presence of the large number of Eastern American maritime plants in the James Bay region. All other routes are open to many objections on botanical grounds. LaRocque has shown that the Lake St. John connecting route is open to only one palæontological objection; the lack of evidence. This he attributes to an absence of palæontological exploration in the region between Lake St. John and James Bay. The botanical objections are over-ruled on the basis of considerably greater botanical evidence for the possibility of such a route.

The post-glacial history of the flora of the Hudson Bay region may be reconstructed as follows: The arctic species moved southward from their refuge north of the glacial boundary, or northward from their refuge south of the glacial boundary. Their present arctic concentration, as well as their absence elsewhere, may be attributed to their fitness to the environment.

The Eastern American maritime species are presumed to have entered the region via the shores of a post-Pleistocene marine connection between James Bay and the Gulf of St. Lawrence. The non-maritime species of Eastern American affinities followed the general northward migration of species from south of the glacial boundary when the climate became much warmer northward (anathermal and extending through the hypsothermal).

The Western American maritime species followed the arctic shore southward to their present position. Non-maritime Western American species entered the area either from the northwest or southwest (mainly the latter).

Eastern-Western American Disjuncts followed the same routes or may have arisen from remnants of populations that survived glaciation south of the glacial boundary in eastern America. These have persisted only in very special localities. This may be attributed to their ecological specificity, but little is known concerning this.

Widespread Boreal and Subarctic species, whether maritime or non-maritime, followed suitable habitats of the opening land left by the shrinking of the glaciers. It is largely the greater ecological amplitude of these species that reduced the number of available habitats and consequently has diminished the number of species of other phytogeographic groups in the area.

Flint (1957) notes that the belt of postglacial marine sediments bordering Hudson Bay averages 150 miles in width, and the recent map of the Geological Association of Canada (1958) clearly shows this (*see* map X). The persistent coastal belt provided a pioneer habitat continuously, for as the old raised beaches were colonized by the encroaching forest, new bare areas were exposed by crustal upwarping.

Possibly some of the most significant data concerning the rapidity of colonization of such bared areas will come from the work that has been begun by Moir (1954) on the "fossil" strand lines on the Hudson Bay lowland.

The continued presence of the pioneer habitat of the sea shore for the dispersal of arctic, arctic-alpine, and maritime species is significant, serving as an important migration route for the species mentioned above as well as providing a continuing habitat for the bulk of the arctic and subarctic species of the flora. Griggs (1940) and Stebbins (1942), among others, have emphasized the importance of the pioneer habitat in the persistence of Arctic-alpine and Disjunct Eastern American species beyond their "natural" range.

It should be noted, however, that the vicissitudes of competition and continued migration to the newly exposed sites must have served to diminish the number of species, since the particular habitat may not have been available for an already dwindling population. Thus, in the Churchill region, tiny populations of *Alopecurus alpinus*, *Hierochloë pauciflora*, *Arabis alpina*, etc. persist precariously where suitable niches are available. Their extension of area is dependent on the persistence and extension of the ecologically suitable habitat. Thus, should the rising coast continue to shrink Hudson Bay and the forest encroach on the present coastal tundra, it is very possible for these relict colonies to be eliminated, as doubtless relict colonies of other species of similar habitat specificity were destroyed in the past. As Stebbins (1942) noted, such small populations would probably possess little genetic variability, and consequently would be confined to a highly specific ecological niche.

If the assumptions and calculations of Gutenberg (1941) are correct, the Hudson Bay region still has about 250 metres to rise before complete crustal recovery from the effects of the Pleistocene ice takes place. This means that Hudson Bay will become much smaller. It is reasonable to assume that a high proportion of the species of presently restricted range will disappear with the extension of the coast northward. This would also be hastened by the encroachment of forest with disappearance of the effects of the bay ice on the climate of the region. It is likely, however, in the event that this does happen, that a high proportion of the species will persist on the continuing pioneer habitat of river and lake shores and on exposed rock masses.

A closer knowledge of the flora and vegetation around Hudson Bay may hold the key to the history of the flora in more southern portions of glaciated North America.

Acknowledgments

The writer wishes to thank all those who rendered help in the course of this work; especially Eva Beckett, Howard A. Crum, Ilmari Hustich, E. Lepage, D. A. Livingstone, D. R. Moir, A. E. Porsild, J. C. Ritchie, Jacques Rousseau, and H. J. Scoggan. To the Defense Research Board of Canada I should like to offer particular thanks for the accommodations and laboratory space during the course of the field work. The entire project was financed by the National Museum of Canada and was done in co-operation with Dr. H. A. Crum, without whose help and encouragement the work could not have been accomplished.

Vascular Plants New to the Manitoba Flora

All collections cited, except those of Mrs. Eva Beckett, have been deposited in the National Herbarium of Canada, Ottawa. Mrs. Beckett's collections are in her private herbarium, Fort William, Ontario. The abbreviation "S & C" refers to the collections that W. B. Schofield and H. A. Crum made during the summer of 1956 under the auspices of the National Museum of Canada.

Festuca prolifera (Piper) Fern.

In spruce forest of stream margins and among willow thickets at upper margin of salt marsh. Fort Churchill (B. R. Irvine & D. McFarlane, 234), Churchill (S & C, 7090), Goose Creek, near Fort Churchill (form with pilose lemmas, S & C, 6969). Since the form with pilose lemmas occurs wherever the typical form is present, and since it differs from it only in this very minor character, it can be considered no more than a form. It has been named var. *lasiolepis* Fern., *Rhodora* 35: 136 (1933). The above species is probably that alluded to by Scoggan (1957), page 92.

Temperate Amphi-Atlantic: mts. of N. H., n. to Gaspé Pen., Que., Cape Breton I., N. S., w. Nfld., n. Que., s. along w. coast of Hudson Bay to James Bay and n. to Churchill, Man.; Scotland.

Alopecurus alpinus L.

Dampish mossy tundra saddle, outcrop ridge between Churchill and Fort Churchill (S & C, 6817). This marks the first authentic record of this species from Manitoba (*see* Scoggan, 1957, p. 121).

Arctic-subarctic circumpolar: n. Alaska, n. Yukon, across n. Mackenzie and Keewatin Districts and throughout the Canadian Arctic Archipelago, n. Quebec, Labrador, Greenland, its southernmost North American station at Cape Henrietta Maria, Ont.; Spitsbergen, n. Eurasia. A map of the American distribution is given by Porsild (1957, map 15).

Hierochloë pauciflora R. Br.

Very local on damp mossy tundra of slope near pond, Fort Churchill (S & C, 6889).

Arctic widespread: n. Alaska, n. Yukon, n. Mackenzie and Keewatin Districts, Banks, Victoria, Baffin and Devon I., absent from the northern Queen Elizabeth Islands (Ellesmere, Cornwallis, etc.) and absent from Greenland, southward along the western Hudson Bay coast to Cape Henrietta Maria, Ont.; scattered in arctic Eurasia. A map of the American distribution is given by Porsild (1957, map 14).

Kobresia myosuroides (Vill.) Fiori & Paol.

Frost boils and dryish open tundra, Eskimo Point, near Churchill (S & C, 6920) and Fort Churchill (S & C, 7027).

Arctic-alpine, circumpolar: Alaska, Yukon and in the mts. to New Mexico, Mackenzie and Keewatin Districts, Canadian Arctic Archipelago (not known from the w. Queen Elizabeth Is.), n. Quebec-Labrador, Greenland; Iceland, n. Europe in mts. of Scandinavia, in central Europe from the Pyrenees to the Caucasus, n. Asia, and also extending southward in the central Asiatic mts. A map of the American distribution is given by Porsild (1957, map 68).

Carex ursina Dew.

Rare on edge of open saline flats, Churchill (S. & C. 7082).

High-arctic maritime, circumpolar: coastal n. Alaska, n. Yukon, scattered along the coast of Mackenzie District and on the Hudson Bay coast of Keewatin District to Churchill, Man., scattered in Canadian Arctic Archipelago and on side of Hudson Bay at Cape Jones (?); and in n. Quebec, central e. and w. Greenland; Spitsbergen, Franz Josef Land, Vaygach, Novaya Zemlya, and local at the mouth of the Ob and Khatanga rivers in Asia. A map of the American distribution is given by Porsild (1957, map 77).

Betula minor (Tuckerm.) Fern.

Spreading shrub to 11 feet, with D.B.H. of 4 inches, in dry birch-willow scrub of gravel ridge, Twin Lakes Hill, about 20 miles e. of Churchill (S & C, 7117). Only one shrub was seen, suggesting that this is near the northeastern extreme of its range. The plant was heavy with fruit, but no reproduction was observed from previous years.

Temperate Eastern American: montane n.e. N. Y. and n.e., to Laurentide Mts., Que., Gaspé, Nfld., Quebec-Labrador, to n.w. Ont. (Trout Lake, Moose R. and Moose Factory) and e. Man. (Churchill).

Koenigia islandica L.

Damp area behind salt marsh, Bird Cove, about 8 mi. e. of Fort Churchill (S & C, 7024).

Arctic-alpine, circumpolar: Alaska, Yukon s. locally in mts. to Colorado, rare in e. Mackenzie Dist. (Bathurst Inlet) and e. Keewatin, s. to Churchill, Man., Baffin I., Devon I. and Southampton I., e. coast of Hudson Bay s. to Fort George, Que., and s. on Labrador coast to *ca.* lat. 55° N, Greenland; Iceland, Jan Mayen, Spitsbergen, n. Eurasia; s. Tierra del Fuego. A map of the American distribution is given by Porsild (1957, map 128).

Salicornia europaea L.

Salt-marsh mud flats, Cockle's Point, west side of Churchill River, near Churchill (S & C, 6904). Plants were immature when collected so that they cannot be referred to either of the varieties known from Hudson Bay region (var. *simplex* (Pursh) Fern. or var. *prostrata* (Pall.) Fern.). Also noted on e. side of Churchill R.

Temperate circumpolar halophyte: coastal e. America from Ga. n. to Nfld. local inland in halic habitats of Mich., Wis., and Ill., James Bay n. to Churchill, Man., coastal w. America from S. Calif. n. to B. C. and s. Alaska (Anchorage) and inland Calif. in alkaline marshes of the desert; Eurasia (largely s.w. and maritime); N. and S. Africa.

Suaeda ?maritima (L.) Dumort.

Mud flats of salt marsh, Cockle's Point, w. side of Churchill R., near Churchill (S & C, 6903), also noted locally on e. side of Churchill R. The specimens were immature, so that the species name is uncertain. *S. americana* (Pers.) Fern. is known from the James Bay region, and the above plants may ultimately prove to be that species.

Temperate Amphi-Atlantic (?) maritime: coastal e. America from Va. n. to e. Que., coastal w. America on s. Pacific coast, coast of Mackenzie Dist., Hudson Bay at Churchill, Man.(?); coastal Europe from Norway and s. Finland to Scotland and s. to the Mediterranean; N. Africa.

Montia lamprosperma Cham.

Damp area of upper salt marsh. About 5 mi. e. of Fort Churchill (S & C, 6729), Fort Churchill (S & C, 6792), Cockle's Point, w. side of Churchill R., near Churchill (S & C, 6913).

Subarctic circumpolar: Pacific coastal Alaska and s.w. Yukon, local along the arctic shore of Mackenzie and Keewatin Districts to Hudson Bay, s. Baffin I., s. along shores of Labrador Pen. to Nfld., N.S. and Me., s. Greenland; Iceland, n. Eurasia. A map of the American distribution is given by Porsild (1957, map 131).

Minuartia rossii (R. Br.) House

Dry dunes south of Fort Churchill (E. Beckett, August 3, 1950). This collection consists of a single plant.

North American arctic-alpine: Alaska and Yukon, s. in mts. to the Rocky Mts. of Colorado, e. through the Canadian Arctic Archipelago, with an isolated station at Churchill, Man., n. Greenland. A map of the American distribution is given by Porsild (1957, map 149).

Ranunculus hyperboreus Rottb.

In water of pools on the beach and tundra. Fort Churchill (S & C, 6512, 6791, 6990), Bird Cove, 8 mi. e. of Fort Churchill (S & C, 7040).

Arctic-subarctic alpine, circumpolar: Alaska, Yukon, s. to the Canadian Rockies, Mackenzie and Keewatin Districts and Canadian Arctic Archipelago, coastal Labrador Peninsula, n. Nfld., Greenland; Iceland, Spitsbergen, Novaya Zemlya, n. Asia. A map of the American distribution is given by Porsild (1957, map 165).

Eutrema edwardsii R. Br.

Damp tundra along the coast. Fort Churchill (E. Beckett, August 9, 1955, S & C, 6629, 6823), Christmas Lake area (B. R. Irvine, 196), Eskimo Point, w. side of Churchill R., near Churchill (S & C, 6911). Arctic, circumpolar: Alaska, Yukon, e. through Mackenzie and Keewatin Dist. and the Canadian Arctic Archipelago, s. to Churchill, Man., n. Quebec-Labrador, Greenland (absent in s.); Spitsbergen, Novaya Zemlya, n. Eurasia. A map of the American distribution is given by Porsild (1957, map 178).

Hutchinsia procumbens (L.) Desv.

Forming thick colonies among stones and on gravel, damp area of beach above tide level, and on the margin of the coastal salt marshes, about 5 mi. e. of Fort Churchill (S & C, 6764), near East Creek, about 4 m. e. of Fort Churchill (S & C, 6944), Goose Cove, about 8 mi. e. of Fort Churchill (S & C, 7041). This plant is extremely tiny and inconspicuous (to 5 cm. max. height in the area) and can be readily overlooked.

Widespread circumboreal (bipolar): mts. of Alta., B. C. s. to Colo., Nevada to s. Calif., n. Nfld. and s. Lab., Churchill, Man.; Europe; central Asia; N. Africa; Australia; Chile.

Draba aurea M. Vahl

Dry gravelly area of outcrop ridge and gravel ridge inland. Churchill (E. Beckett, July 20, 1956), Twin Lakes Hill, about 20 mi. e. of Fort Churchill (S & C, 7128).

Subarctic-alpine, Eastern-Western American Disjunct: Alaska, Yukon s. in mts. to Colorado, e. to Black Hills, S. Dak., local in Mackenzie Dist., w. coast of Hudson Bay (Churchill) and around James Bay, n. Labrador, s. Greenland.

Draba luteola Greene

Sand dunes, Fort Churchill (S & C, 6494).

Western American alpine: Alaska, Yukon, s. in mts. to Utah and Colorado, e. to Great Bear Lake and Coronation Gulf, Mack. Dist., and Churchill, Man.

Arabis alpina L.

Willow-lined bank of pond at foot of esker, Christmas Lake area (B. R. Irvine, 205, 203).

Subarctic amphi-Atlantic: Gaspé Pen., Que., n. to w. Nfld., n. up Labrador and w. down e. coast of Hudson Bay, n.e. Manitoba (Christmas Lake), Southampton I., s. Baffin I., s. Greenland; mts. of Europe (Alps, Carpathians, Urals, Pyrenees); Siberia; Himalayas. A map of the American distribution is given by Porsild (1957, map 196).

Galium trifidum L. var. *halophilum* Fern. & Wieg.

Swamps behind beach and upper edge of salt marsh. Fort Churchill (S & C, 6628, 6857), about 5 mi. e. of Fort Churchill (S & C, 6830a), Bird Cove, about 8 mi. e. of Fort Churchill (S & C, 6938). The above report is included with some reservations, since material of this variety, when immature, coincides precisely with *G. brandegei* Gray. The latter species was discussed in some detail by M. P. Porsild (1930). Fernald (1950) distinguishes these taxa on the basis of leaf shape, but the dimensions he gives (.7–2 cm long vs. 6–12 mm long) overlap almost entirely, and leaf-shape is extremely variable, dependent on habitat. It is singular, however, that the collections from Churchill that are referred to as *G. trifidum* var. *halophilum* come from near the sea, largely from distinctly saline or brackish habitats. It is possible, therefore, that *G. brandegei* is absent in the Churchill flora. There is need of a good deal of collecting in late summer to clear up this problem, as well as others, in the Churchill flora.

Eastern North American maritime: Coast of Mass. n. to Que., Nfld., and s. e. Lab., coast of Hudson Bay (?).

NOTEWORTHY PLANTS NEW TO CHURCHILL

All reports below refer to extension of range within Manitoba, the information on previous range being based on the *Flora of Manitoba* by H. J. Scoggan. The abbreviation *N* denotes an extension of range northward from the "northernmost collection" of the *Flora of Manitoba*. The locality in brackets indicates the previous northernmost locality, with the page on which it appears in the *Flora of Manitoba.*

Equisetum palustre L.

In pond near road, Landing (Farnsworth) Lake, Fort Churchill (S & C, 6765), on wet bank, same locality (S & C, 6766).

N (York Factory, Scoggan, p. 49).

Sparganium multipedunculatum (Morong.) Rydb.

In pond-porridge mud of dried-up pond in spruce woods, Twin Lakes Hill, about 20 mi. e. of Fort Churchill (S & C, 7135).

N (Riding Mountain, Scoggan, p. 70). This supports the report of Bell (1880) mentioned by Scoggan: "Nelson River between Lake Winnipeg and the coast of Hudson Bay."

Zostera marina L. var. *stenophylla* Aschers. & Graebn.

Hudson Bay coast on the way to Fox Island, Churchill (H. Ellis, July 1950; in the herbarium of Eva Beckett).

Scoggan (p. 72) notes that there is no Manitoba specimen of this species, although it was reported from "the mouth of the Churchill River" by Lowe (1943). The above collection indicates its presence near the region Lowe cites. Fox Island is a coastal island approximately 20 mi. e. of Churchill.

Arctophila fulva (Trin.) Rupr.

Streamlet on gravel sea-beach, Fort Churchill (S & C, 6511, 6610, 7055), lush growth around small pool near high tide mark, 3 mi. e. of Fort Churchill (B. R. Irvine & M. D. McFarlane, 219).

Otherwise reported in Manitoba only from Baralzon Lake (Scoggan, p. 102). The Churchill collections represent the southernmost Manitoba collections (although Porsild, 1957, has a dot on his distribution map indicating that the plant is known from near Churchill).

Catabrosa aquatica (L.) Beauv.

Damp brackish swamp near sea, about 5 mi. e. of Fort Churchill (S & C, 6731), wet area near seep, gravel sea-beach, Fort Churchill (S & C, 7049, 6885), damp humus muck behind salt marsh, Bird Cove, 8 mi. e. of Fort Churchill (S & C, 7025), small depression near road through tundra, same locality (S & C, 7023).

N (York Factory, Scoggan, p. 103). The material of this species is extremely variable in stature, dependent on fertility or wetness of the habitat. Our number 7025 consists of robust, geniculately creeping plants, rooting at the nodes, whereas the plants represented by number 7023 are very tiny (*ca.* 7 cm tall) and rooting only at the base. Even in different parts of the same site a variety of growth forms may be noted. The characters that Fernald used to segregate var. *laurentiana* from var. *uniflora* are very minute and subject to variation dependent on habitat. Those used to distinguish var. *uniflora* from the polymorphic species suffer from the same faults, so that it seems wisest to consider this species as a large and variable one.

Eleocharis acicularis (L.) R. & S.

Wet brackish area of beach, Fort Churchill (S & C, 7054), humus mud of Goose Creek bank (S & C, 7014).

N (Cochrane River, Scoggan, p. 143). Reference to map 66 in Porsild (1957) gives a clearer picture of the Canadian distribution of this species than the Svenson map cited by Scoggan and shows the considerable progress made in botanical exploration of northern Canada in the past twenty years.

Carex livida (Wahl.) Willd., var. *grayana* (Dew.) Fern.

Open swamp of tundra, about 3 mi. s. of Fort Churchill (S & C, 6723), damp depressions of tundra near Lake Isabella, Fort Churchill (S & C, 6861). Not uncommon in the wet tundra of the region.

N (Camp Hughes, near Brandon, Scoggan, p. 180). The above collections note a conspicuous northern extension of range.

Lemna minor L.

In pools and backwaters of Goose Creek (S & C, 7013).

N (Hayes River near the west end of Knee Lake, Scoggan, p. 195).

Juncus bufonius L. var. *halophilus* Buch. & Fern.

Forming thin red mats in open areas of salt marsh, Bird Cove (S & C, 6943, 7028), gravel near Landing (Farnsworth) Lake, near Fort Churchill (S & C, 7103).

N (Gillam, Scoggan, p. 199).

Listera cordata (L.) R. Br.

Mossy hummocks in spruce-larch woods, Fort Churchill (S & C, 6726).

N (York Factory, Scoggan, p. 224).

Spergularia mariana (L.) Griseb.

Brackish sea-beach, about 5 mi. e. of Fort Churchill (S & C, 6746, 6858), salt marsh, Bird Cove, about 8 mi. e. of Fort Churchill (S & C, 7032).

N (Dawson Bay, Lake Winnipegosis, Scoggan, p. 270). This is a considerable northern extension.

Potentilla anserina L.

Gravel ridge facing pool behind beach, Fort Churchill (S & C, 6882).

N (York Factory, Scoggan, p. 346).

Oxytropis terrae-novae Fern.

In his map of the distribution of this species, Porsild (1957) has placed a dot that is very close to the Churchill area (*See* his map 250).

Cicuta bulbifera L.

Wet humus swamp near Goose Creek, Fort Churchill (S & C, 7008).

N (Reindeer Lake, Scoggan, p. 416).

Naumburgia thyrsiflora (L.) Duby.

Banks of Goose Creek (S & C, 7012).

N (Reindeer Lake, Scoggan, p. 440).

Mentha arvensis L. var. *villosa* (Benth.) Stewart

Fairly common along wet stream-bank, Warkworth Creek, Churchill (J. M. Gillett, 2540, S & C, 7005).

N (Gillam, Scoggan, p. 472).

Valeriana septentrionalis Rydb.

Deep shade of willows near bank of Goose Creek (S & C, 7006), abundant in mossy areas among willows of lowland black spruce forest. Twin Lakes Hill, about 20 mi. e. of Fort Churchill (S & C, 7143).

N (York Factory, Scoggan, p. 504).

Antennaria rosea (D. C. Eaton) Greene

Dryish base of outcrop ridge, Eskimo Point, w. side of Churchill River, near Churchill (S & C, 6931).

N (Reindeer Lake, Scoggan, p. 535).

Senecio indecorus Greene

Humus on shelves of outcropping ridge, Eskimo Point, w. side of Churchill River, near Churchill (S & C, 6932), damp open area near Tidal about 5 mi. s. of Churchill (S & C, 6962). The above species was reported by Ritchie (1956) but was inadvertently omitted from Scoggan's *Flora of Manitoba*.

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DRYAS BABINGTONIANA, nom. nov. An Overlooked Species of the British Isles and Western Norway

A. E. PORSILD

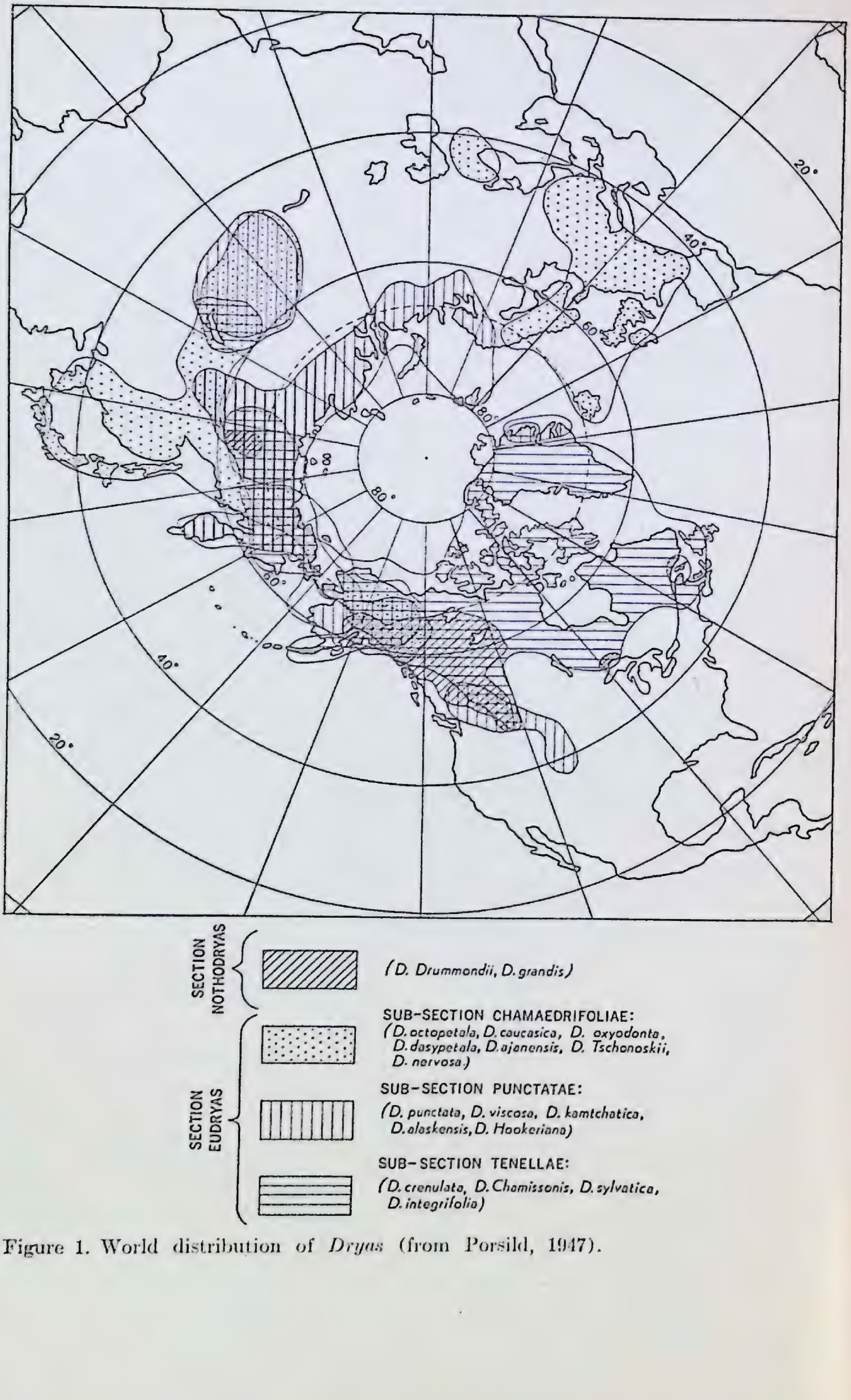
The old, holarctic genus *Dryas* in the family *Rosaceae* was long thought to comprise one circumpolar species, *D. octopetala* L. besides the largely North American *D. integrifolia* M. Vahl and the wholly North American, yellow-flowered *D. Drummondii* Richards. In his revision, S. V. Juzepczuk (1929) divided the genus into NOTHODRYAS Juz. and EUDRYAS Juz. In the first he placed the North American *D. Drummondii* Richards., *D. tomentosa* Farr (*D. Drummondii* var. *tomentosa* (Farr) Williams), and the East Asiatic *D. grandis* JUZ. EUDRYAS he divided into three sub-sections: *Chamaedrifoliae* Juz., *Punctatae* Juz., and *Tenellae* Juz. He described *D. Hookeriana* (in the subsection *Punctatae*), endemic to the North American central Rocky Mts., but lacked material for an adequate treatment of the genus in North America. The writer (1947) in his revision of the North American members followed Juzepczuk's subdivision and characterization of the genus.

The section NOTHODRYAS, which Juzepczuk believed older than EUDRYAS, is represented by D. *grandis* Juz. in eastern Asia and by *D. Drummondii* in North America. The latter, at least, is very well separated from all members of the section EUDRYAS by such fundamental characters as the flattened receptacle, hairy filaments, and yellow petals. The constant presence on the peduncles of vestigial bracts, which not infrequently support abortive, lateral flowers, suggests derivation from ancestral forms of the *Dryadeae*. Its present main area is in the west, from central Alaska east to Mackenzie distr. and south to Mont. and Ore., but isolated populations in the Great Lakes Region and in the Gulf of St. Lawrence, far east of its present main area, suggest a former more extensive continuous range.

The section EUDRYAS comprises three subsections:

1. Subsection *Chamaedrifoliae* typified by *D. octopetala* s. str. (Iceland, Faeroes, mts. of Scandinavia, centr. Europe, British Isles, Pyrenees, Balkan, and Asia Minor, arctic Eur. and Asia, and barely entering NW. America); *D. oxyodonta* Juz. (mts. of western, central, and eastern Siberia); *D. dasypetala* Juz. (endemic to Alatau and Soongoria); *D. caucasica* Juz. (endemic to Caucasus); *D. ajanensis* Juz. (endemic to mountains of Okhotsk Sea region, E. Siberia); *D. Tschonoskii* Juz. (mts. of Sakhalin and N. Japan); *D. nervosa* Juz. (endemic to mts. of N. Korea).

2. Subsection *Punctatae* is mainly palearctic: *D. punctata* Juz. (arctic Europe to arctic E. Siberia south to mts. of N. Mongolia–Soongoria, also in mts. of Alaska-Yukon and arctic NW. America and NE. Greenland); *D. viscosa* Juz. (endemic to Lena-Kolyma region of E. Siberia); *D. Hookeriana* (endemic to Rocky Mts. and Cascades between lat. 40° and 53°N); *D. alaskensis* Porsild (endemic to mts. of Alaska-Yukon).


20°
40°
60°
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80°
60°
40°
20°
SECTION NOTHODRYAS
(D. Drummondii, D. grandis)
SECTION EUDRYAS
SUB-SECTION CHAMAEDRIFOLIAE:
(D. octopetala, D. caucasica, D. oxyodonta, D. dasypetala, D. ajanensis, D. Tschonoskii, D. nervosa)
SUB-SECTION PUNCTATAE:
(D. punctata, D. viscosa, D. kamtchatica, D. alaskensis, D. Hookeriana)
SUB-SECTION TENELLAE:
(D. crenulata, D. Chamissonis, D. sylvatica, D. integrifolia)

Figure 1. World distribution of *Dryas* (from Porsild, 1947).

3. Subsection *Tenellae* is almost wholly nearctic; it comprises five species and is probably the youngest and most recently evolved. The most aggressive and widespread of these is *D. integrifolia* M. Vahl, which in postglacial time has reoccupied practically all of the northeastern parts of North America which were overrun by the ice during the Pleistocene. It is not known from the East Asiatic mainland but has been collected on Wrangel Island. It is a rare plant in the Canadian Rocky Mountains, where it is restricted to high mountains south approximately to latitude 53°. In Atlantic North America it is isolated in Newfoundland, Gaspe, and Anticosti Island; it is common on the west and north coasts of Greenland, somewhat local on the northeast coast, and absent except in the central part of the southeast coast. *D. Chamissonis* Spreng. ex Juz. is endemic to the Bering Sea region and the N. Pacific coast of Alaska; *D. sylvatica* (Hult.) Porsild is endemic to central Alaska-Yukon and the Mackenzie District; *D. crenulata* Juz. is known from NE. Siberia, Alaska, Yukon east to Mackenzie Delta.

The fifth species: *D. Babingtoniana,* nom. nov., based on *D. octopetala,* β *pilosa* Bab., is endemic to western and northwestern Ireland, Scotland, and Norway. Local populations have been tentatively identified from northwest and northeast Greenland. In Iceland and the Faeroe islands, *D. octopetala,* although otherwise typical, in the length and spacing of its style hairs has an important character in common with *D. Babingtoniana* and other members of the subsection *Tenellae.*

World distribution of *Dryas* is known in map fig. 1 and the outline of leaves of representative species of all sections and subsections in Plate I.

When revising the North American members of the genus *Dryas* (Porsild, l. c. 1947) I was unable to compare certain critical material from Alaska-Yukon and from northeast Greenland with representative material of some of Juzepczuk's newly described species from eastern Asia. I was anxious, therefore, when visiting European herbaria during the winter 1954–1955, and again in 1957–1958 to examine as much Asiatic material as possible.[1]

While examining the rich collections of *Dryas* at Kew, I discovered, among the material of *D. octopetala* from the British Isles, a plant collected in 1946, in the county of Clare, Ireland, which differed from *D. octopetala* in some important characters and, following the classification of Juzepczuk, should be placed in the subsection *Tenellae.* A further search, continued later in other herbaria, soon disclosed not only that this plant was well represented in a number of other herbaria, but that it is native to Scotland as well as Ireland and is found very locally on the west coast of Norway and perhaps also in northeast Greenland.

In this search I was greatly aided by the curators of a number of herbaria. I particularly wish to thank Professor J. D. Matthews, Keeper of the herbarium of the University of Aberdeen; Professor D. A. Webb, curator of the herbarium of Trinity College, Dublin, who kindly examined for me *Dryas* in the Dublin herbaria; Dr. E. F. Warburg, Druce Curator,

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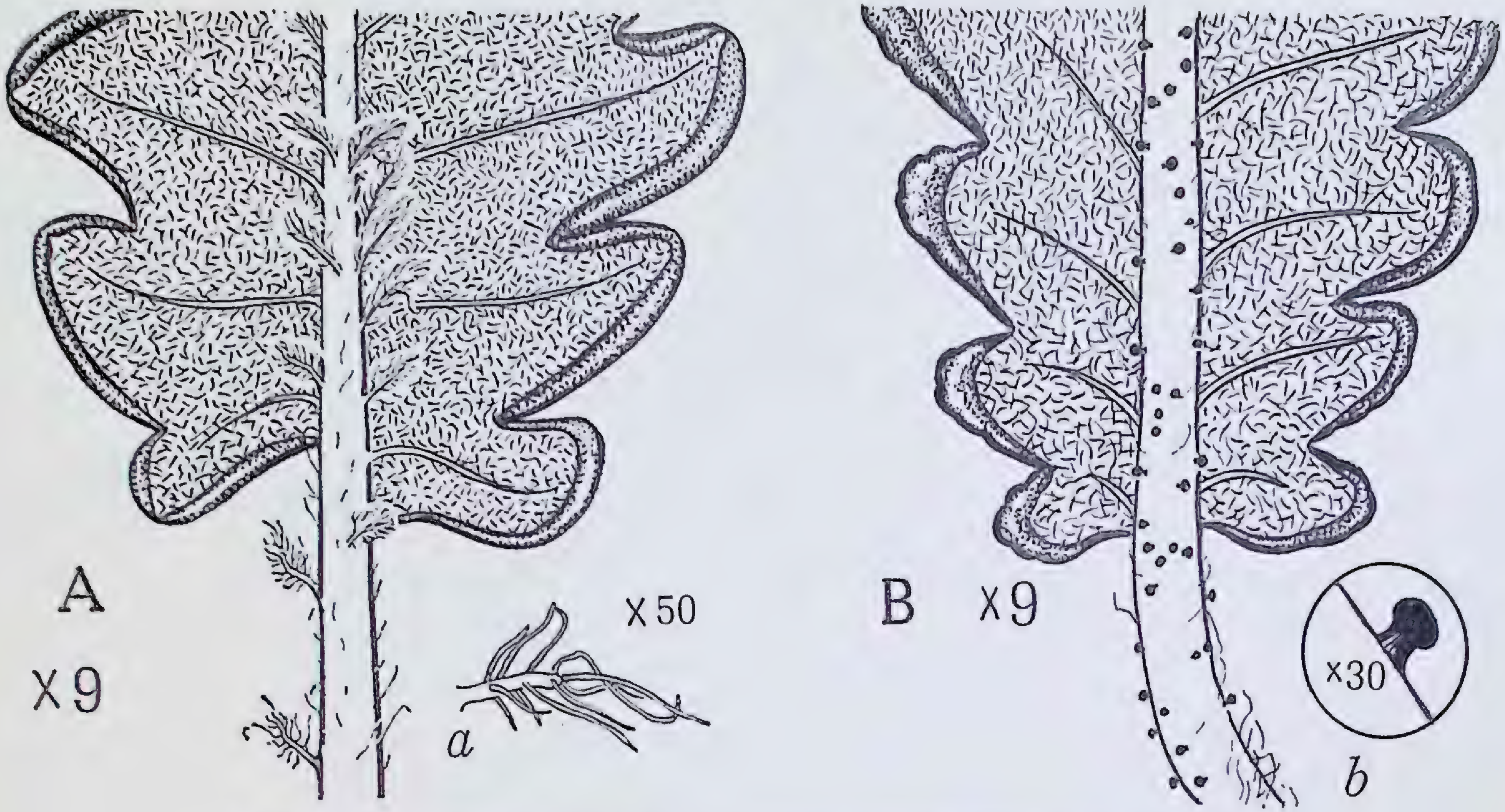

Figure 2. A—Underside of leaf in D. *octopetala* showing branched hairs. *a*. Much enlarged branched hair (fig. a from Jessen, 1921).
B—Underside of leaf in *D. Hookeriana* showing naked glands. *b*. Enlarged gland.

University of Oxford; Dr. S. M. Walters, curator of the herbarium of the University of Cambridge, who kindly lent *Dryas* specimens from Babington's Herbarium; Dr. G. Taylor, then Keeper of Botany, British Museum (Natural History); Dr. O. Hagerup, curator of the herbarium of the University of Copenhagen, Denmark; Dr. Johannes Lid, then Curator of the University herbarium, Oslo, Norway; Dr. O. Gjaerevoll, curator of the herbarium of the Norwegian Academy of Sciences, Trondheim, Norway; Dr. E. Hultén, director of the botanical department of Naturhistoriska Riksmuseum, Stockholm, Sweden, and Dr. A. Kalela, director of the Botanical Museum, Helsinki, Finland. It is a pleasure also to record my thanks to Professor B. K. Schischkin, Director of the Komarov Botanical Institute, Leningrad, for facilitating my work at the Komarov Institute, and to Dr. S. V. Juzepczuk who greatly aided me in my examination of the Asiatic species of *Dryas* in the Leningrad herbarium. I am very much indebted also to Mr. N. Y. Sandwith of Kew, without whose generous help I should not have been able to decipher and identify the handwriting of a number of old labels nor to locate place names unfamiliar and obscure to me.

Following the discovery, my first task was to examine current British and Irish manuals for a clue to the identity of the curious *Dryas* from County Clare. When this failed, I suspected, perhaps not unnaturally, that I might have before me a new and undescribed species. However, a further search through the older British literature soon disclosed that the Clare plant had indeed been recognized more than a hundred years ago by the Irish botanist, J. T. MacKay, as distinct from *D. octopetala* and that it had been formally described as *D. octopetala* β *pilosa* by Babington (1842), who the following year included it in his Manual of British Botany (1843) where it was carried through eight editions, only to be dropped in the posthumous ninth edition, and apparently was forgotten or ignored by subsequent students of the flora of the British Isles.

The history of β *pilosa* is briefly as follows: Babington, in 1836, visited the Dublin Botanic Garden where he was shown "two forms of *Dryas octopetala*," one of them from Benbulben, County Sligo, and the other from County Clare, which J. T. Mackay for some years had grown in the Garden. In 1840, Babington himself visited Benbulben where he obtained additional material from the station from which Mackay's specimens had been taken. Babington (1842) reported the discovery, giving full credit to Mackay "for having been the first to observe that a considerable difference existed between these plants, and it was by his kind permission that I had the opportunity of examining the growing plants in the College Botanical Garden at Dublin, and making from them the outline accompanying this paper."

Babington (l.c. p. 182) first considered the characters observed to be only those of varieties, as follows:

"*Dryas octopetala* (Linn.) Leaves crenate-serrate, obtuse; flowers white.

α. Sepals three or four times as long as broad, acute, covered with red hairs; base of the calyx hemispherical; under side of the petiole bearing minute, linear, pellucid, hairy scales mixed with long hairs; leaves ovate-oblong, deeply cut into large rounded lobes; under side of the petiole and midrib green. (Pl. vii, fig. 1).

> I have seen specimens of this variety from Teesdale, Breadalbane, Clova and Southerland; also from Munich, Mount Stockhorn and the Col de Voza in Switzerland, the Pyrenees and Calabria.
>
> β. *pilosa*. Sepals three or four times as long as broad, slightly pointed, covered with nearly black hairs; base of the calyx hemispherical; petiole hairy, but without scales; leaves oblong or ovate-oblong, deeply cut into large slightly acute lobes; under side of the petiole and midrib dark red. (Pl. vii, fig. 2).
>
> I have only seen cultivated specimens of this variety obtained from the county of Clare in Ireland.
>
> γ. *depressa*. Sepals twice as long as broad, blunt and rounded at the end, covered with red hairs; base of the calyx truncate, nearly flat; under side of the petiole as in var. α; leaves ovate, deeply cut into large rounded lobes; under side of the petiole and midrib green. (Pl. vii, fig. 3).
>
> I have gathered this plant on Ben Bulben in the county of Sligo, Ireland, but have not seen specimens from any other place."

Babington laid much emphasis on the relatively short and broad sepals and the truncate, nearly flat base of the calyx in var. *γ*, as compared with the longer and narrower sepals and hemispherical calyx in vars. *α* and *β*, but he also appears to have been the first to observe and describe the more important "linear, pellucid, hairy scales" which are always found on the midrib and petiole of *D. octopetala* (fig. 2 and 2a)[1] and other members of the subsection *Chamaedrifoliae* Juz. as well as in *D. punctata* Juz. but totally lacking in all members of subsection *Tenellae* as well as in members of the section NOTHODRYAS.

In his manual, Babington (1843) took up his varieties *α* and *β* under *D. octopetala*. To the descriptions already given, he now added that in var. α "linear, pellucid fringed scales" are found on the underside of the midrib as well as on the petiole, while in var. *β* the underside of the petiole and the midrib are "dark red, hairy but without scales," and the "Awn longer and more feathery." The var. *γ*. *depressa* was elevated in the manual to the rank of full species. To the earlier description was added "I have not seen recent petals, but suspect that they are yellowish." However, in the 5th edition of the manual (1862) *D. depressa* was again reduced to var. *γ* with the comment: "This is now generally believed to be only a variety of *D. 8-petala*," and in the 6th edition it was dropped altogether because "It now appears that *D. depressa* (Bab.), first separated by the late J. T. Mackay, has no constant characters." The varieties *α* and *β* however, were maintained, but dropped altogether in the 9th, posthumous edition.

This action is scarcely justified, for, after examining the material of *Dryas* from the British Isles in the larger British herbaria, I am convinced that besides *D. octopetala* s. str., represented chiefly in Scotland and northern Ireland, there is at least one other and equally distinct species (β *pilosa* Bab.), which is the common one on limestone in western Ireland in counties of Clare and Galway and occurs also, but more sparingly, in the counties of Leitrim and Fermanagh, as well as in Scotland in the counties of Sutherland, Perth, W. Ross, Angus, and Aberdeen.

I am uncertain as to the status of *D. depressa* Bab., of which I have seen the type from Benbulben, County Sligo, in Babington's herbarium, besides

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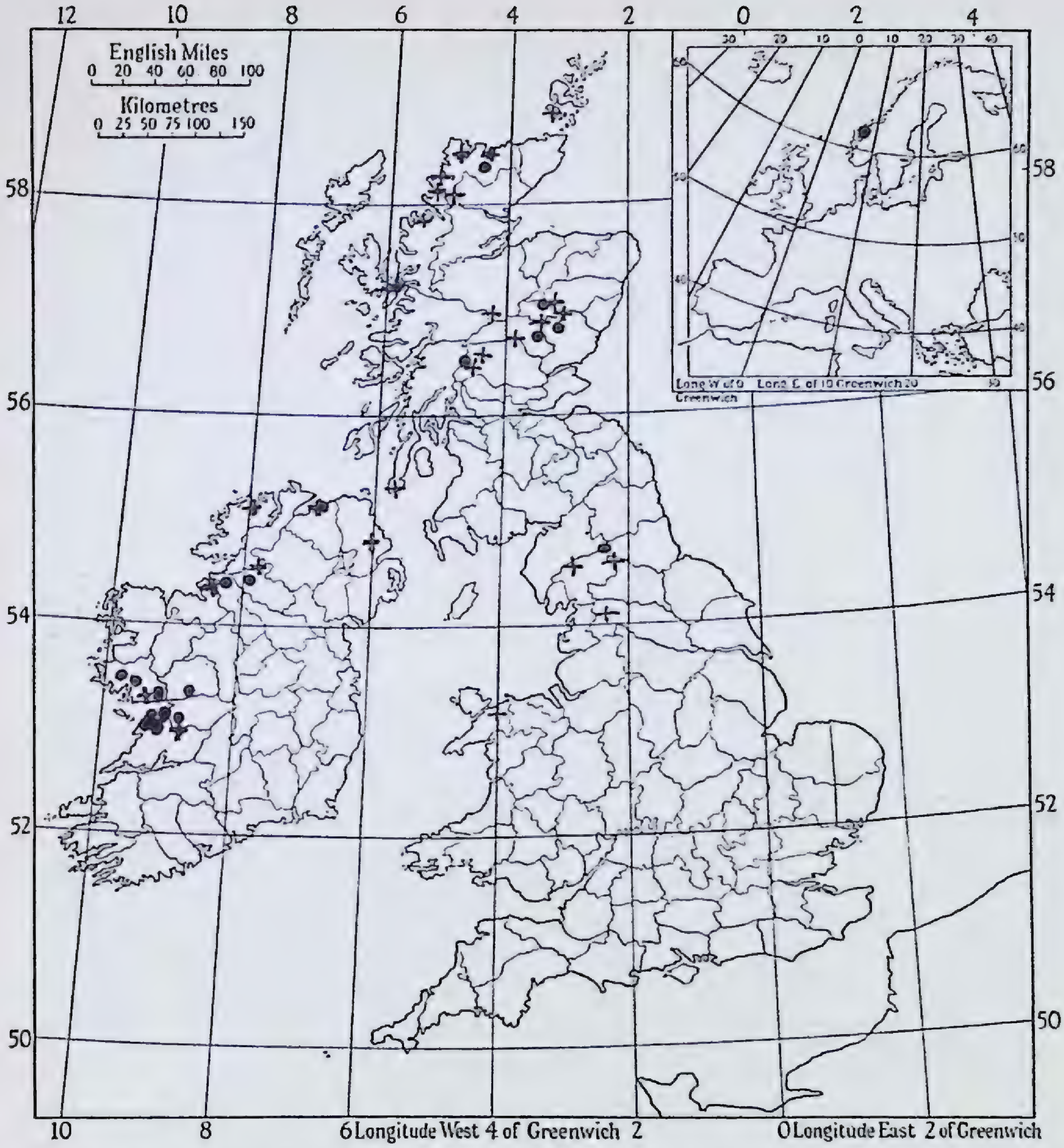
[1] Perhaps first illustrated by Jessen (1921, fig. 27, E, b) who, in the explanation of the figure, by a *lapsus* attributed these peculiar hairs to the upper surface of the leaf, although in the text (p. 70) he correctly states that they are found on the lower surface "upon the larger bundles which project as ribs. . . ."


12
10
8
6
4
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English Miles
0 20 40 60 80 100
Kilometres
0 25 50 75 100 150
58
56
54
52
50
10
8
6 Longitude West 4 of Greenwich 2
0 Longitude East 2 of Greenwich
Long W of 0 Long E of 10 Greenwich 20
Greenwich

Figure 3. Distribution of *D. Babingtoniana* (dots) and *D. octopetala* s. lat. (crosses) in the British Isles.

two other collections, likewise from Benbulben, from Herb. Arthur Bennett (BM). One is undated and was collected by E. F. Linton; the ticket of the other is dated 16 July, 1879, but does not give the collector's name. Both are a close match for the type (Pl. II, B) and in habit and in the outline of the leaves bear a general resemblance to var. *pilosa* Bab., from which they differ mainly in the presence of branched hairs on the lower surface of the midrib and petioles. Three other Benbulben collections were reported to me by Dr. Webb, in the Dublin National Herbarium (1880, Moore; 1882, Vowell; and 1884, Barrington & Vowell). The last appears to be the most recent collections of *Dryas* from Benbulben. According to Dr. Webb the Benbulben station is on "high-level limestone."

Equally uncertain is the plant peculiar to limestone barrens of Yorkshire, of which I have seen a large number of collections, from Teesdale, Arncliffe, and Cronkley Fell. Mr. Sandwith tells me that the Cronkley Fell colony is very small, perhaps only 100 feet across and, like those from Teesdale and Arncliffe, on "sugar limestone." The material I have seen is rather uniform, showing a plant much smaller than either *D. octopetala* s. str. or "var. *pilosa*," with rather deeply incised, often revolute-margined leaves 1.0 to 1.5 cm long, deeply wrinkled, rugose, and sparingly hirsute on the upper surface; the underside is thinly covered by grey felt, and the midrib and petioles bear scattered, branched hairs. The scapes are short and stiff, often barely overtopping the leaves, and the flowers are smaller than in typical *D. octopetala*, averaging 1.5 to 2.0 cm in diameter. Some collections are labelled "var. *depressa* Bab.," to which plant they bear but slight resemblance. One collection in the National Herbarium, Ottawa, is labelled "Teesdale, Yorks, sugarlimestone, H. T. [?] Warnell" and bears the following additional note: "form smaller and distinct from our Scotch plant." To me the Yorkshire plant looks very much like that occurring along the north coast of Siberia, in Spitsbergen, Novaya Zemlya, and NE. Greenland, and variously reported as *D. octopetala*, *D. octopetala* var. *minor*, *D. punctata*, and *D. incisa* Juz. It will probably prove to be genetically distinct from *D. octopetala* s. str.

While the taxonomic status of the Benbulben and Yorkshire plants is thus as yet uncertain, there is ample reason for considering var. *pilosa* Bab. distinct from *D. octopetala* s. str. and for placing it in subsection *Tenellae* Juz., otherwise not represented in the flora of Europe; and I believe it will be entirely appropriate to name it for C. C. Babington, who first described it:

Dryas Babingtoniana nom. nov. (subsect. *Tenellae* Juz.)
D. octopetala, β *pilosa* Bab. 1842, Ann. Nat. Hist., London, 183, Tab. vii, fig. 2. Tab. I, 5, II, and III.

Densely matted. Leaves leathery, firm, ovate, $1\frac{1}{4}$ to 2 times longer than broad, 1.5 to 2.4 cm long, 0.6 to 1.2 cm broad, broadest below the

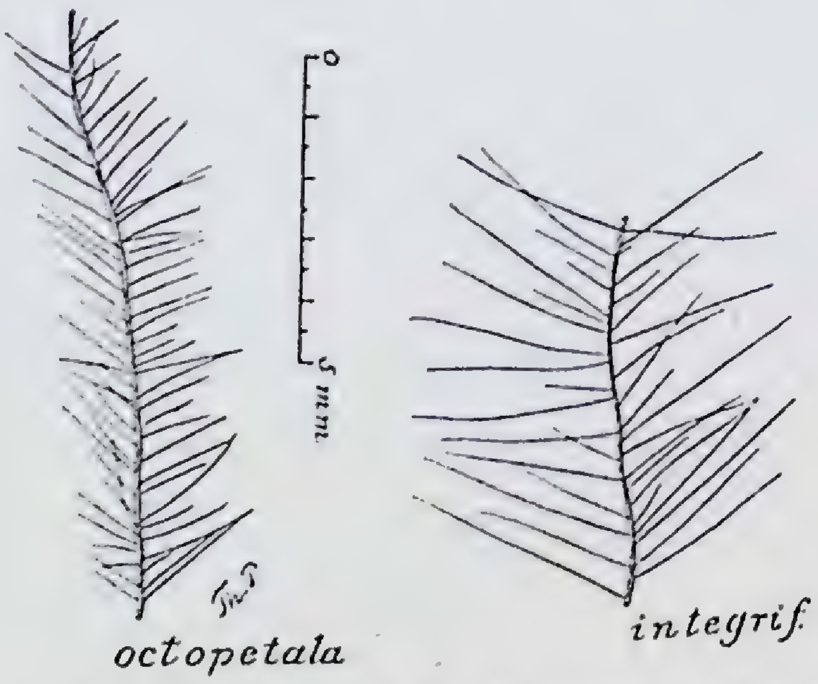

Figure 4. Style hairs in *D. octopetala* and *D. integrifolia* (after Th. Porsild, 1920).

middle; the tip rounded or acute, the base sub-cordate or truncate, rarely rounded, coarsely and somewhat irregularly crenate-dentate, in well-developed leaves with from 6 to 7 teeth to each margin. In dried specimens the upper leaf surface is dark green, dull, glabrous, or with a few white hairs along the mid-vein, rugose with deeply impressed veins. The underside is white-tomentose, its midrib well covered by soft, white hairs but entirely lacking brown, stalked glands or branched hairs. Petioles as long as the blade, thinly white-tomentose, lacking stalked glands or branched hairs; stipules prominent. Scapes, at time of floration, 3 to 4 cm long, becoming up to 12 cm long in fruit, sparingly tomentose, with a single, filiform bract below the middle; the upper part bearing naked, gland-tipped brown hairs. Flowers 3.0 to 3.5 cm in diameter; sepals linear-lanceolate, 8 to 10 mm long, 2 to 2.5 mm wide, acute, sparsely covered dorsally by black, gland-tipped hairs, pilose along the margins; petals obovate-elliptic, white, twice as long as the sepals; fruit about 3 mm long, pilose; mature style 2.5 to 3.0 cm long, its hairs spreading, averaging 2.5 mm in length with about 30 hairs per millimetre of style.

TYPE: *in cult.* Bot. Garden in Dublin (from Co. Clare), 11 July, 1836, in Herb. C. C. Babington (CGE). Plate III.

DISTRIBUTION: British Isles: Ireland: Counties of Clare, Galway, Leitrim, and Fermanagh. Scotland: Counties of Sutherland, Perth, W. Ross, Angus, and Aberdeen. England: doubtful in Yorkshire. Norway: Möre on the west coast. Greenland: northern E. & W. coast (?).

The map fig. 3 and the list of specimens cited at the end of this paper show that the distribution in the British Isles of *D. Babingtoniana*, broadly speaking, is similar to that of *D. octopetala*, but judging from the admittedly sparse information on the labels, it is a pronounced calciphile whereas *D. octopetala*, although favouring calcareous soils, is not restricted to limestone soils.

Some indication of the local abundance of *D. Babingtoniana* in the counties of Clare and Galway of western Ireland may be deduced from herbarium labels and from the writings of J. T. Mackay (1806) who stated, when undoubtedly referring to the plant he had transferred to the Botanic Garden in Dublin: "This plant covers whole mountains of limestone on the estate of Blindon Blood, Esq., in the barony of Burren, county Clare where there is scarcely any other vegetable to be seen." *D. Babingtoniana* is still common there, for specimens at Kew labelled *D. octopetala*, collected in 1946, at Carnsefin, Blackhead, by S. Ross-Craig and J. Robert Sealy, bear the following annotation: "Forming a carpet over limestone rock, often the principal constituent in continuous sward over the rocks of the mountainside." In all probability the very first record of *Dryas* from anywhere in the British Isles applies to *D. Babingtoniana*, for according to Clarke (1900) the plant which the Reverend Richard Heaton saw and, according to How (1650), recorded "In the mountains betwixt Gort and Galloway. It makes a pretty shew in the winter with its rough heads like *Viorna*," is a *Dryas*.

It is worth recalling that Babington (1843) noted that the styles of his *β. pilosa* were "longer and more feathery" than those of *D. octopetala* because, in the subsection of *Tenellae* of EUDRYAS, and also in members of NOTHODRYAS, the hairs of the fully mature styles are longer and more openly spaced than in *D. octopetala* and other members of the subsections *Chamae-*

arifoliae and *Punctatae*. Believing that the style hairs afforded a reliable character by which fruiting arctic material of *D. octopetala* could be separated from *D. integrifolia* (Fig. 4), Th. Porsild (1920) undertook a statistical examination of the styles in the *Dryas* material available in the herbarium of the Arctic Station at Disko, Greenland, supplemented by material borrowed from the Botanical Museum at Copenhagen. In presenting the results of his survey, he noted that in *D. octopetala* from east Greenland, Iceland, and the Faeroe Islands, the number of hairs per millimeter of style averaged 28.9 against 38.8 in *D. octopetala* from the British Isles, 37.3 from northern Eurasia, 38.8 from North America, 42.5 from the Alps, and 53.2 from the Pyrenees, and that the average length of the style hairs in East Greenland, Iceland, and the Faeroe Islands was 1.94 mm, against 1.64 mm in Eurasia and North America. A careful check made by the writer in 1954 of a much larger and more representative sample than that upon which Th. Porsild based his results, confirmed the general trend of differences reported. In *D. Babingtoniana* the average length of the style hairs was found to be 2.5 mm and the spacing about 30 hairs per millimeter of style, or somewhat higher values than those reported by Th. Porsild in *D. integrifolia* from North America and Greenland.

A search for *Dryas Babingtoniana* in British and European herbaria, in 1954–55, indicated that it is apparently absent on the Continent. However, in 1958, in the herbarium at Trondheim, I found three collections, all from the Möre area on the west coast of Norway. This is of particular interest because the Möre area is thought to have been unglaciated during the Pleistocene and hence is one of the important coastal mountain refuges for west arctic elements in the Scandinavian flora (E. Dahl, 1946 and 1955). In Iceland and the Faeroe Islands *D. octopetala* appears normal, except in the style character mentioned above. An examination in 1954 and 1957 of the copious material of Greenlandic *Dryas* in the University herbarium at Copenhagen disclosed a number of collections from Franz Joseph Fiord in E. Greenland, between lat. 73° 30′ and lat. 74° 06′ which, by the shape and incision of the leaf, the absence of branched hairs on the underside of midrib and petioles, and in the length and spacing of the style hairs, closely approach *D. Babingtoniana.* This is undoubtedly the plant reported from the east and north coasts of Greenland by Holmen (1957) and Böcher, Holmen, and Jakobsen (1957) as *D. Chamissonis* Juz. On phytogeographic as well as climatic grounds, the presence in high arctic parts of Greenland of *D. Chamissonis,* otherwise known only from oceanic parts of the southern Bering Sea and NW. Pacific area, seems as unlikely as the presence of the equally oceanic *D. Babingtoniana* in Franz Josephs Fiord's collections in East Greenland. Possibly a further study of the Greenland plant will prove it distinct.

Clapham, Tutin, and Warburg (1952) reported the chromosome number in British *D. octopetala* to be 2n=18, and Jørgensen, Sørensen, and Westergaard (1958) report n=9 in flower buds from Clavering Island in East Greenland. Böcher and Larsen (1950) reported 2n=18 in *D. integrifolia* from the SW. coast of Greenland. As far as I know, no chromosome counts have been reported for other species of *Dryas.* The fact that two species, as well separated as *D. octopetala* and *D. Drummondii,* each belonging in different sections, may be artificially crossed to form *D. Sündermanii,* may indicate the absence of genetical barriers in the genus.

List of specimens of *Dryas Babingtoniana* in British herbaria, 1955; additional specimens in Dublin herbaria (marked *) were kindly reported to me by Dr. D. A. Webb of Trinity College. For the sake of completeness I have added material of *Dryas Babingtoniana* seen by me in 1955–56 and 1957–58 in other herbaria. Abbreviations indicating the herbaria in which the specimens were seen are those of *Index Herbariorum,* 1956:

Dublin, Trinity College (TCD); Dublin, National Herbarium (DBN); Aberdeen University (ABD); Cambridge University (CGE); Oxford University, Druce Herb. (OXF); British Museum (Nat. Hist.) (BM); Kew (K); Copenhagen University (C); National Herbarium, Ottawa (CAN); Trondheim, Norway (TRH); Naturhistoriska Riksmuseum, Stockholm, Sweden (S).

IRELAND

V.C. Hib. 9 CLARE: Black Head, Ballyvaughan, 1898, T. J. Foggit (BM); 1853, E. T. Bennett, (BM); 1885, R. P. Murray (BM); 1875, S. A. Stewart (BM); 1862, Thos. Wright (BM); 1865, no collector, (K); 1935, H. S. Redgrave (K); 1949, E. Hultén (S); Corkscrew Rd., 1891, H. C. Levinge (K, DBN*); Carnsefin, 1946, S. Ross-Craig & Robert Sealy, No. 1335 (K, S, TCD*); Cappennawalla, *ca.* 1 mile SW. of Ballyvaughan, 1946, S. Ross-Craig & Robert Sealy, No. 1365 (K); 1876, S. A. Stewart (ABD, BM); 1909, C. G. Druce (S, OXF); 1849, T. G. B. Osborn (OXF); Burren, 1894, P. B. O'Kelly (BM); no date, E. Bennett (OXF); 1911, C. H. Ostenfeld, (C); 1884, Scully (DBN*); 1895 and 1907, Praeger (DBN*); 1862, Wright (DBN*); s. of Black Head, 1880, Barrington (DBN*); Gleninagh, 1895, Praeger (DBN*); 1911, C. Lindman (S); Poulsallagh, 1936, P. M. Hall (K, BM); Muckanagh Lough, 1905, R. L. Praeger (BM); Valley s. of Ballyvaughan, 1925, A. J. Wilmott, No. 2340 (BM).

S. E. GALWAY: Esker Lough, 1899, Praeger (DBN*); Castle Taylor 1870, Dowd (DBN*); 1892, H. C. Levinge (OXF, BM, DBN*); 1850, Blake (DBN*); 1886, A. E. Lomax (OXF); 1831, H. Blake (BM) Blakes Hill, no coll., 1858 (BM, OXF); Gort, 1865, Wright (TCD*).

W. GALWAY: Gentian Hill, 1889, Praeger (DBN*); Benlettery, 1895, Johnston (DBN*); Ardrehaw, 1885, R. P. Murray (BM); Gentian Hill, 1930, 1933, 1935, 1937, 1943, 1945, Pearson (TCD*); Athenry, 1865, Wright (TCD*)

LEITRIM: Glenade, 1905, Praeger (DBN*).

FERMANAGH: Poulaphuca, 1904, Praeger (DBN*).

SCOTLAND

SUTHERLAND: W. Sutherl. near Inchadamph, 1929, A. J. Wilmott, Nos. 3374 & 3381 (BM); 1833, W. W. Campbell (BM); Assynt, 1836, J. Macnab (BM); Betty Hill, 1907, C. G. Druce (OXF).

PERTH: Ben Lavigh, Mid-Perth, 1889, E. S. Marshall (BM); 1880, Peter Ewing (BM); Grampian, 1879, F. M. Webb (BM).

V.C. 89 E. PERTHSHIRE: Limestone outcrops NE. of Cairnwell, 2650 feet, 1939, P. M. Hall, No. 3642 (BM).

W. ROSS: Cnochan, 1894, C. E. Druce (OXF).

V.C. 90 ANGUS: Glen Dole, Clova, Forfarshire, 1895, T. C. Goggit (BM); 1922, E. G. Beach (K); 1832, Wm. Brand (BM); 1831, Wm. Brand (ABD); Glen Fiadh, Clova, 1872, T. Drummond (K); Carnlochan Glen, Forfarshire, Don T. Farquharson (ABD); Corrie Dhubh Galair, Breadalbane, 1900, J. Fraser (K).

ABERDEEN: Little Craigandal, Braemar, 1879, J. W. H. T. (ABD); 1855, N. S. (ABD); 1935, E. C. Wallace (K); 1854, A. Croall, Pl. of Braemar, No. 18 (ABD, K); 1855, no collector (BM); Ben Liu, 1879, Tyndrum (BM); 1936, A. H. & G. H. A. (K); Craignadalsby, 1889, Ed. F. Linton (BM).

ENGLAND

YORK: Arncliffe, Yorkshire, 1844, Settle (OXF)

V.C. 65 N.W. YORK: Cronkley Fell, 1921, W. C. Worsdell (K). The collection consists of three sterile scraps on which the leaves lack branched hairs on the midrib. This and the preceding collection are with much doubt referred to *D. Babingtoniana.*

NORWAY

Möre-Romsdal fylke, abt. lat. 62° 40′ N.—long. 3° 30′ W. Fraena, Talströhesten, 1952; O. Gjaerevoll; Eide, Lyngsted, *idem,* 1952; Hustad, Slepskaret, *idem,* 1954 (TRH).

GREENLAND

The following specimens are tentatively referred to *D. Babingtoniana:* East coast between 73° 30′ and 74° 06′ N. Gauss Pen., Sørensen Nos. 5040, 5049, 5069, and 5085; Clavering Isl., *idem* Nos. 5526, 5526b, and 5504; Ymer Isl., *idem* Nos. 3175-6 and 3171d; Hudson Land, *idem,* No. 5195 (all C); Andree Land, Aug. 14, 1929, Vaage (O, CAN); Andree Land, Seidenfaden. No. 807 (NY). North West Coast: Thule, Feachem, No. 253 (BM); Etah, 1934, Humphreys (BM).

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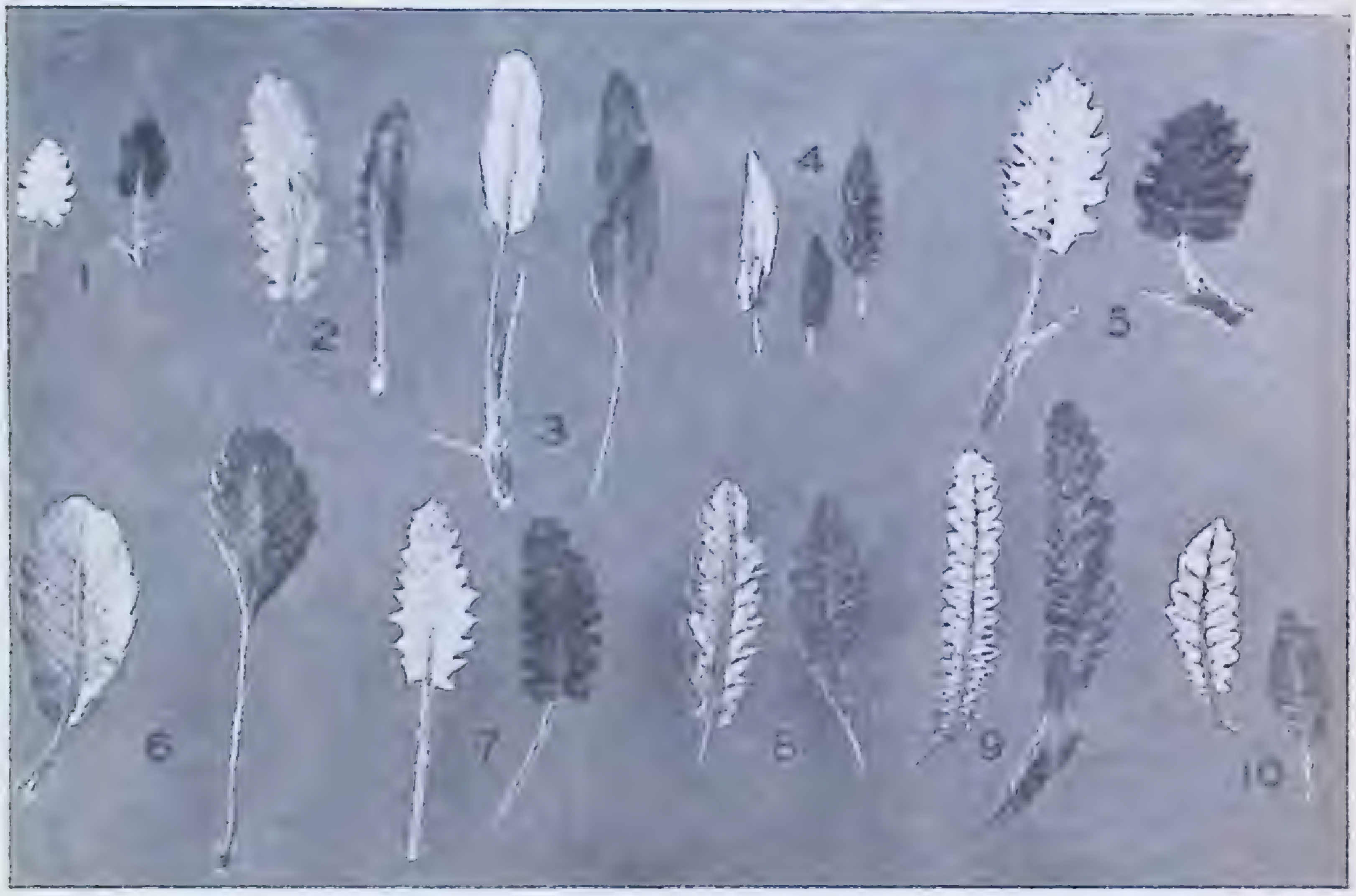
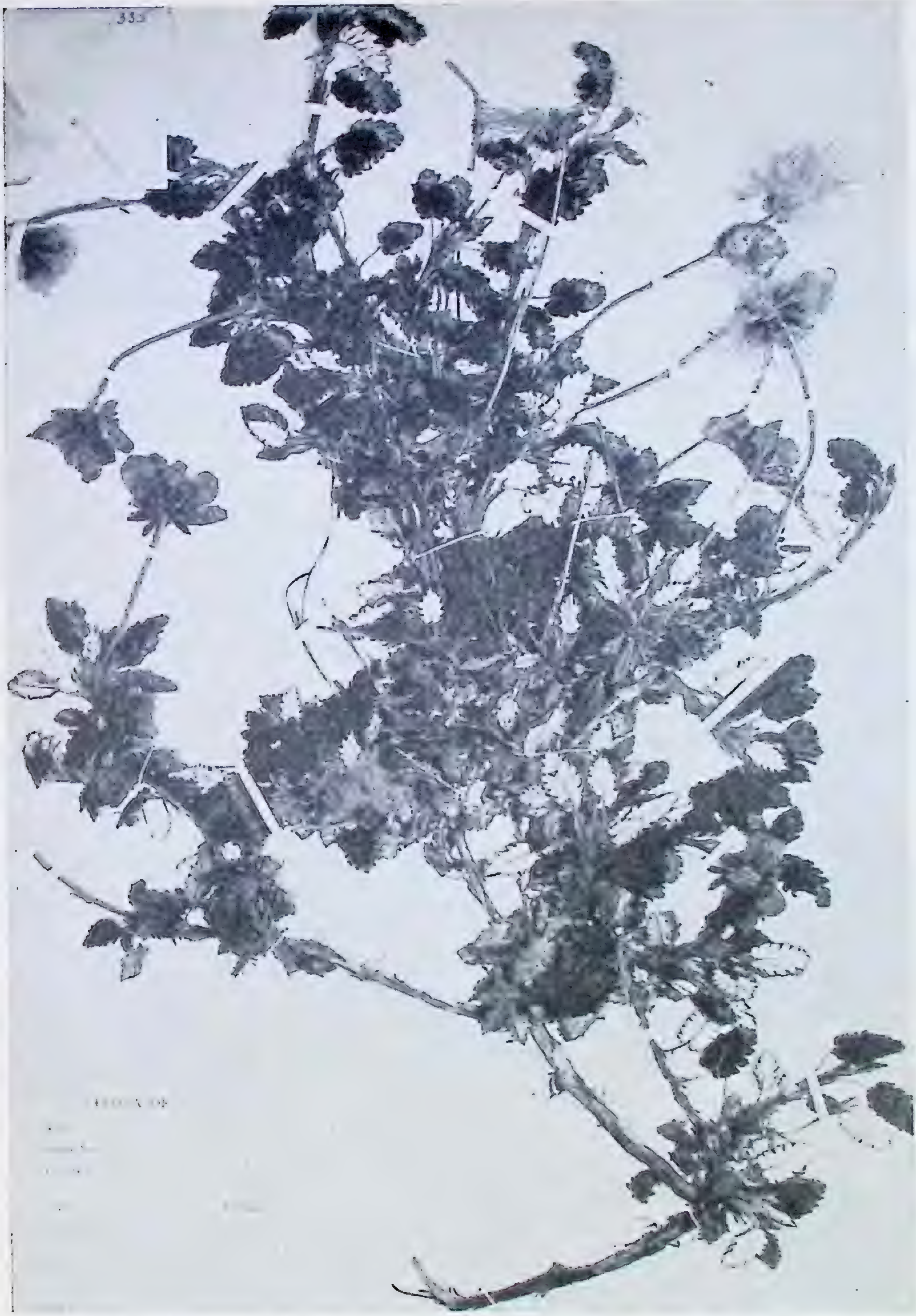
Plate I



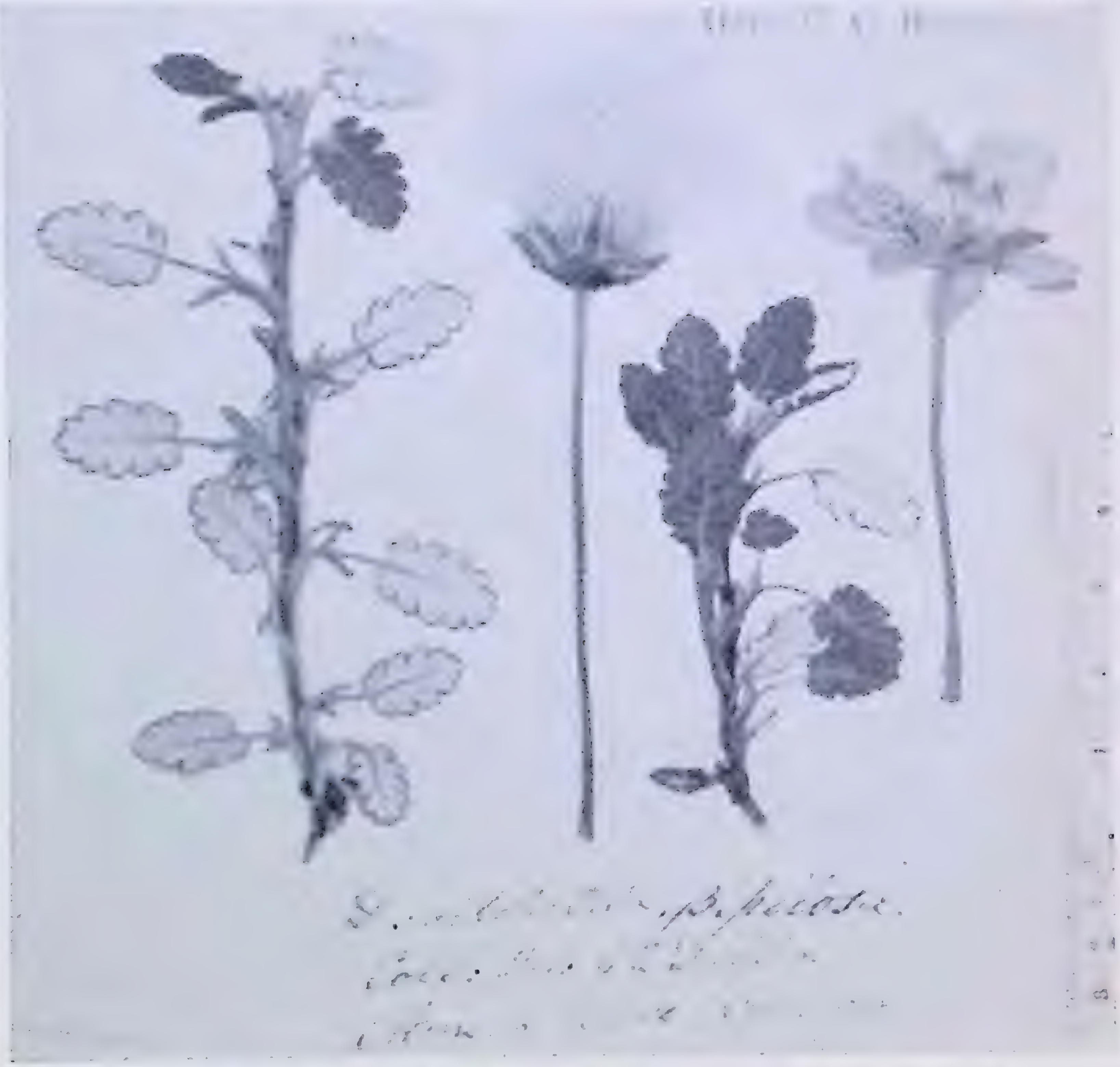
Outline of leaf-blades in *Dryas*: 1. *D. Chamissonis* Spreng.; 2. *D. crenulata* Juz.; 3. *D. sylvatica* (Hult.) Porsild; 4. *D. integrifolia* M. Vahl; 5. *D. Babingtoniana* Porsild (all subsection *Tenellae* of EUDRYAS); 6 *D. Drummondii* Richards. (NOTHODRYAS); 7. *D. octopetala* L. s. str. (EUDRYAS, subsection *Chamaedrifoliae*); 8. *D. punctata* Juz.; 9. *D. alaskensis* Porsild; 10. *D. Hookeriana* Juz. (all subsection *Punctatae*). All approx. $\frac{4}{5}$ nat. size.

PLATE II



Dryas Babingtoniana, approx. ½ nat. size from Co. Clare, Ireland, Ross-Craig & Sealy, No. 1335. (K)

Plate III



The type of *D. Babingtoniana* Porsild (*D. octopetala* β. *pilosa* Bab.) from Babington's herbarium (CGE). Nat. size.